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Effects of fire intensity on groundcover shrubs in a frequently burned longleaf pine savanna

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EFFECTS OF FIRE INTENSITY ON GROUNDCOVER SHRUBS IN A FREQUENTLY BURNED LONGLEAF PINE SAVANNA

A Dissertation

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DEDICATION

For my wife,

who sees magic in every flower.

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ABSTRACT

Variation in fire intensity may affect the structure and composition of frequently burned plant communities. I hypothesize that small-scale variation in fuel loads affects fire intensity within single fires in frequently burned savannas. Furthermore, I expect that local differences in fire intensity produce predictable patterns to the demography of groundcover shrubs. I tested these hypotheses by manipulating fuel loads in a longleaf pine savanna. Fuel load treatments consisted of fine fuel removal, pine needle addition, wood addition and unaltered control, mimicking naturally occurring fuel load variation. Treatments were repeated in $1m^2$ subplots over two sets of biennial burns and shrub responses were followed for 5 years. Addition of fuels increased fire intensity (maximum fire temperature, fuel consumption, heat output), while removal of fuels decreased fire intensity relative to controls. For all species pooled, addition of fuels, particularly wood, increased damage to shrubs and decreased resprouting relative to control. Removal of fuels did not affect shrub resprouting. Similarly, fuel addition increased the probability of species loss (genet mortality), while fuel removal had no effect. Fuel addition decreased resprouting of native rhizomatous resprouting species relatively more than that of native root-crown resprouting species or non-native species. However, density of rhizome sprouting shrubs tended to increase over the course of the study. The demography of *Rhus copallinum*, a common rhizomatous species, was affected by fuel load treatments. Matrix projection models indicated that population growth was positive in the control treatment, nearly stable in the pine needle addition treatment, and negative in the fuel removal and wood addition treatments. In all treatments, stasis of large ramets was the largest contributor to population growth. Effects of fuel loads and fire intensity on population dynamics of *R. copallinum* may result from an interaction between damage to rhizomes and post-fire environmental conditions.

My overall results indicate that small-scale variation in fuel loads predictably affects local fire intensity in pine savannas. By altering fire intensity, fuel loads alter patterns to the local demography of shrubs. Small-scale variation in fire intensity may contribute significantly to the observed patterns of shrub abundance in frequently burned pine savannas.

CHAPTER 1

INTRODUCTION

Concepts regarding the relationship between natural disturbances and the composition and structure of plant communities have changed over the past several decades. Earlier studies focused primarily on natural disturbances as catastrophic events that remove all individuals from a site and reinitiate succession (e.g. Clements 1916, Weaver and Clements 1938, Margalef 1963, Odum 1969). However, most field studies have shown that some individuals survive even the most intense disturbances (Turner et al. 1997, del Moral and Grishin 1999, Platt et al. 2000). Furthermore, effects of single large-scale disturbances tend be spatially variable (Walker et al. 1991, Turner et al. 1997, Platt et al. 2002). Consequently, more recent concepts have focused on disturbances as recurrent, potentially predictable events that affect communities over both ecological and evolutionary time (Connell 1978, Pickett et al. 1987, Platt 1999). In this context, characteristics of natural disturbance regimes become important to predicting disturbance effects on communities. Disturbance regimes can vary in characteristics such as frequency, timing, and intensity. Experimental studies of the effects of variation in characteristics of natural disturbances are lacking for many community types.

Fires are a recurrent natural disturbance in many plant communities worldwide. In communities where fires occur more than once during the lifespan of individual plants, many plants survive and potentially reproduce after fires (Whelan 1995, Platt 1999, Bellingham and Sparrow 2000). For example, established individuals of many woody species in fire-frequented savannas either survive most fires outright by thick fire resistant bark (Platt et al. 1988, Glitzenstein et al. 1995, Gignoux et al. 1997, Kennedy and Potgeiter 2003) or resprout from underground organs following mortality of aboveground parts (Rebertus et al. 1989, Olson and Platt 1995, Drewa 2003). In these communities, most fires are “non-catastrophic” disturbance events that damage many individuals, kill relatively few and do not tend to remove species

from a site (Abrahamson 1984, Platt and Connell 2003). Nonetheless, even where fires are predictably recurrent, fire regimes may be variable in frequency, timing and intensity (Rebertus et al. 1993, Drewa et al. 2002, Platt et al. 2002, Slocum et al. 2003). A range of species that differ in their life histories can be expected in communities experiencing variable fire regimes (Matlack and Good 1989, Rebertus et al. 1993, Howe 1994, Gignoux et al. 1997). This may account for the coexistence of large numbers of species in some frequently burned communities and leads to the prediction that increasing the frequency of disturbances of a particular type may alter patterns of abundance and composition within a community (Hoffmann 1998, Menges and Hawkes 1998).

Variation in fire intensity may be particularly important to the composition and structure of plant communities that experience frequent fires (Turner et al. 1997, Platt and Connell 2003). Large high intensity fires may result when ignition occurs under extreme weather conditions or on sites where fuels have accumulated as a result of fire suppression (Morgan 1999, Ramos-Neto and Pivello 2000). Within single fires and at smaller spatial scales, variation in fire intensity may occur as a result of locally variable fuels (Williamson and Black 1981, Gibson et al. 1990, Platt et al. 1991, Whight and Bradstock 1999) or topography (Gibson et al. 1990, Franklin et al. 1997). Such variation in intensity, both among and within single fires, may influence plant communities by creating spatially variable patterns to damage and mortality of plants as well as heterogeneous post-fire environments. In communities such as pine savannas where fire frequencies can be as high as every 1-2 years, variation in intensity may be particularly important (Platt 1999).

Longleaf pine savanna is an ideal community in which to study fire effects, because the flora has evolved under the influence of frequent fires. These botanically diverse systems

typically contain an overstory of pines (predominantly longleaf, *Pinus palustris*) and a groundcover with hundreds of species of shrubs, grasses and forbs (Platt 1999). Natural fire regimes are characterized by frequent (several times per decade) lightning fires during the early growing season (Komarek 1964, Christensen 1981, Olson and Platt 1995, Platt 1999). The presence of rapidly accumulating pyrogenic fuels (i.e. pine needles and dead grasses) facilitates fire ignition and spread (Platt et al. 1991). These frequent fires have been commonly characterized as low intensity, during which groundcover plants are top-killed by fires, but resprout quickly from underground storage organs (Garren 1943, Robertson 1962, Sackett 1975, Christensen 1981, 1988, Myers 1990). Although some early authors noted that fires may be of substantially higher intensity after periods of fire suppression that result in large fuel accumulations (Cary 1932, Wahlenberg 1946), little attention has been paid to the potential for significant fire intensity variation within single fires.

In my dissertation, I explore concepts related to variable fire regimes by experimentally manipulating fire intensity and measuring effects on a woody shrub community. Within a longleaf pine savanna in Louisiana, I tested the hypothesis that small-scale variation in fire intensity affects the composition and structure of groundcover shrub communities by altering the demography of resident species. Prescribed fires designed to mimic frequent natural lightning fires in pine savannas have indicated substantial local variations in fire intensity (Williamson and Black 1981, Gibson et al. 1990, Platt et al. 1991, Olson and Platt 1995, Drewa et al. 2002). However, no previous studies have experimentally manipulated fire intensity, independent of either fire frequency or season, and quantified effects on the groundcover community.

In the Chapter 2, I examine the relationship between variation in fuel loads and fire intensity within the context of frequent growing season fires. I hypothesize that fire intensity, even at spatial scales as small as $1m^2$ will be predictable on the basis of the amount and type of fuels available to fires. Furthermore, I predict that damage to shrubs is a function of fire intensity and thereby directly related to fuels. I test these hypotheses by experimentally manipulating fuel loads at small spatial scales. My fuel load treatments mimic the natural variation in fuel loads found in frequently burned savannas. By measuring multiple components of fire intensity (maximum temperature, fuel consumption, heat output per unit area), I am able to correlate fire damage to particular aspects of fire intensity. The experiment is repeated over fires in two different years to determine how weather conditions may affect the relationship between fuels and fire intensity. My results suggest that by affecting fire intensity, small-scale variation in fuels contributes to the environmental heterogeneity in frequently burned savannas.

In Chapter 3, I explore the effects of fuels on post-fire recovery of shrubs. I hypothesize that high fire intensity, produced by addition of fuels, will significantly decrease resprouting and increase mortality of shrubs relative to unaltered controls. Conversely, I expect that removal of fuels will increase shrub resprouting and decrease mortality relative to unaltered controls. This study provides a direct test of the "ambient temperature" hypothesis (Glitzenstein et al. 1995) which suggests that fire season effects on savanna shrubs are primarily a result of differences in fire intensity. Furthermore, I compare fuel and fire intensity effects on different groups of shrubs. Since the response of shrubs to fire intensity may be related to the morphology of underground resprouting organs (Drewa et al. 2002), I compared the response of native root-crown resprouting species to that of rhizomatous resprouting

species. The results of this study show that small-scale variation in fire intensity has significant effects on shrub resprouting and mortality, thus local species diversity in pine savannas may be related to patterns of fire intensity.

In Chapter 4, I construct a stage-structured population model for *Rhus copallinum*, a common rhizomatous shrub of longleaf pine savannas. The goal of this study is to compare the demography of *R. copallinum* in areas that have experienced fires of differing intensity. I use periodic matrices to generate estimates of population growth and elasticity among fuel load treatment populations. The results suggests that local fire intensity affects short term population growth rate and produces spatial variation in the demography of this common shrub.

CHAPTER 2

EFFECTS OF SMALL-SCALE VARIATION IN FUELS ON FIRE INTENSITY AND DAMAGE TO SHRUBS

Introduction

Characteristics of fires are widely recognized to vary at temporal and spatial scales. In ecosystems with a continuous groundcover of flammable herbaceous vegetation (i.e. temperate grasslands, temperate and tropical savannas), fires typically occur frequently; such fires are often characterized as low intensity because successive fires occur before substantial accumulation of fine fuels (Andersen et al. 1998, Platt 1999, Ramos-Neto and Pivello 2000). Such "non-catastrophic" fires typically remove few individuals and no species (Platt and Connell 2003). For example, fires in pine savannas of the southeastern United States historically were ignited by lightning and burned the same areas more than once per decade, most often in late spring or early summer (Komarek 1964, Christensen 1981, Olson and Platt 1995, Platt 1999). These frequent fires have been characterized as low intensity, with groundcover plants top-killed by fires, but resprouting from underground storage organs (Garren 1943, Robertson 1962, Sackett 1975, Christensen 1981, 1988, Myers 1990).

Nonetheless, fire intensity varies among and within frequent fires in grasslands and savannas. For example, variation in fire intensity may result when ignition occurs under extreme weather conditions (Ansley and Jacoby 1998), as well as from long fire-free intervals (Morgan 1999, Ramos-Neto and Pivello 2000), increased fuel production (Williamson and Black 1981, Gibson et al. 1990, Platt et al. 1991, Whight and Bradstock 1999), or variable topography (Gibson et al. 1990, Franklin et al. 1997). In addition, prescribed fires designed to mimic frequent natural lightning fires have produced substantial small-scale variation in fire intensity within the same fire. In pine savannas, maximum fire temperatures can vary as much as several hundred degrees (Williamson and Black 1981, Gibson et al. 1990, Platt et al. 1991, Olson and Platt 1995, Drewa et al. 2002), and consumption of standing biomass can

range from none to complete within the same fire (Cary 1932, Wahlenberg 1946, Slocum et al. 2003).

Small-scale variation in fire intensity within a single fire event has been hypothesized to result from local variation in fuels (Franklin et al. 1997, Ansley et al. 1998). In frequently burned pine savannas, for example, local fuel load variation is affected by canopy trees and groundcover vegetation. Longleaf pine produces long resin-filled needles that are shed frequently (Landers 1991), resulting in accumulation of flammable fine fuel near large canopy trees (Williamson and Black 1981, Platt et al. 1991, Grace and Platt 1995). Away from pines, pine needle densities are lower; fine fuels are primarily herbaceous vegetation (Platt et al. 1991). Furthermore, soil disturbances by animals may produce patches containing reduced biomass of fine fuels within this background fine fuel matrix (Kaczor and Hartnett 1990). Local variation in woody fuels is produced by accumulation of fine and woody fuels from downed trees and branches (Hermann 1993), especially after storms (Liu et al. 1997, Myers and van Lear 1998). Spatial variation in fire intensity may influence damage of vegetation (Stinson and Wright 1969, Wright and Bailey 1982, Franklin et al. 1997, Ansley et al. 1998). Variation in fire intensity has been hypothesized to affect mortality and resprouting, thereby potentially influencing structure and heterogeneity of plant communities (Glitzenstein et al. 1995, Drewa et al. 2002).

In this study, I examined effects of local variation in fuels on fire intensity and damage of vegetation in a frequently burned longleaf pine savanna. I experimentally manipulated types and amounts of fuels prior to fires, then measured changes in fuel consumption, fire temperature and damage to vegetation in subsequent fires. I tested the following hypotheses: 1) Small-scale variation in fire intensity (i.e., at a scale experienced by individual plants) is

predictably related to small-scale differences in types and amounts of fuels; 2) Damage to vegetation is positively correlated with local fire intensity; and 3) Fire intensity and damage to vegetation produced by local variation in fuels varies across elevation gradients and differs among fires occurring in different years. My study indicates that a locally variable non-catastrophic disturbance might create small-scale spatial heterogeneity in effects that might influence diverse pine savanna groundcover plant communities.

Methods

Study Site

This study was conducted in upland longleaf pine savannas at Camp Whispering Pines (30º41'N; 90º29'W), Tangipahoa Parish, in eastern Louisiana (Figure 2.1a). Camp Whispering Pines (hereafter CWP) is used by the Southeast Louisiana Girl Scout Council as a site for Girl Scout field activities and ecological restoration of loess plain longleaf pine savannas at the western edge of the East Gulf Coastal Plain. The terrain is moderately dissected with elevation ranging from 25-50 m above mean sea level. Most soils are well drained Pleistocene aged, fine Tangi-Ruston-Smithdale sands mixed with and capped by deposits of wind-blown loess (McDaniel 1990). Pine savannas at CWP contain a canopy predominantly of longleaf pine that regenerated naturally following logging of large trees in the early 1930's (Noel et al. 1998). There is a diverse, relatively undisturbed groundcover containing grasses (e.g., *Schizachyrium scoparium, S. tenerum, Panicum anceps, P. verrucosum, Aristida purpurescens, Dichanthelium acuminatum, D. angustifolium, D. strigosum, D. dichotomum, Eragrostis spectabilis)*, forbs (e.g., *Aster dumosus, Acalypha graciliens, Pityopsis graminifolia, Rubus trivialis, Solidago odora, Stylosanthes biflora, Helianthus angustifolius, Galactia volubilis, Desmodium lineatum, Gelsemium sempervirens,*

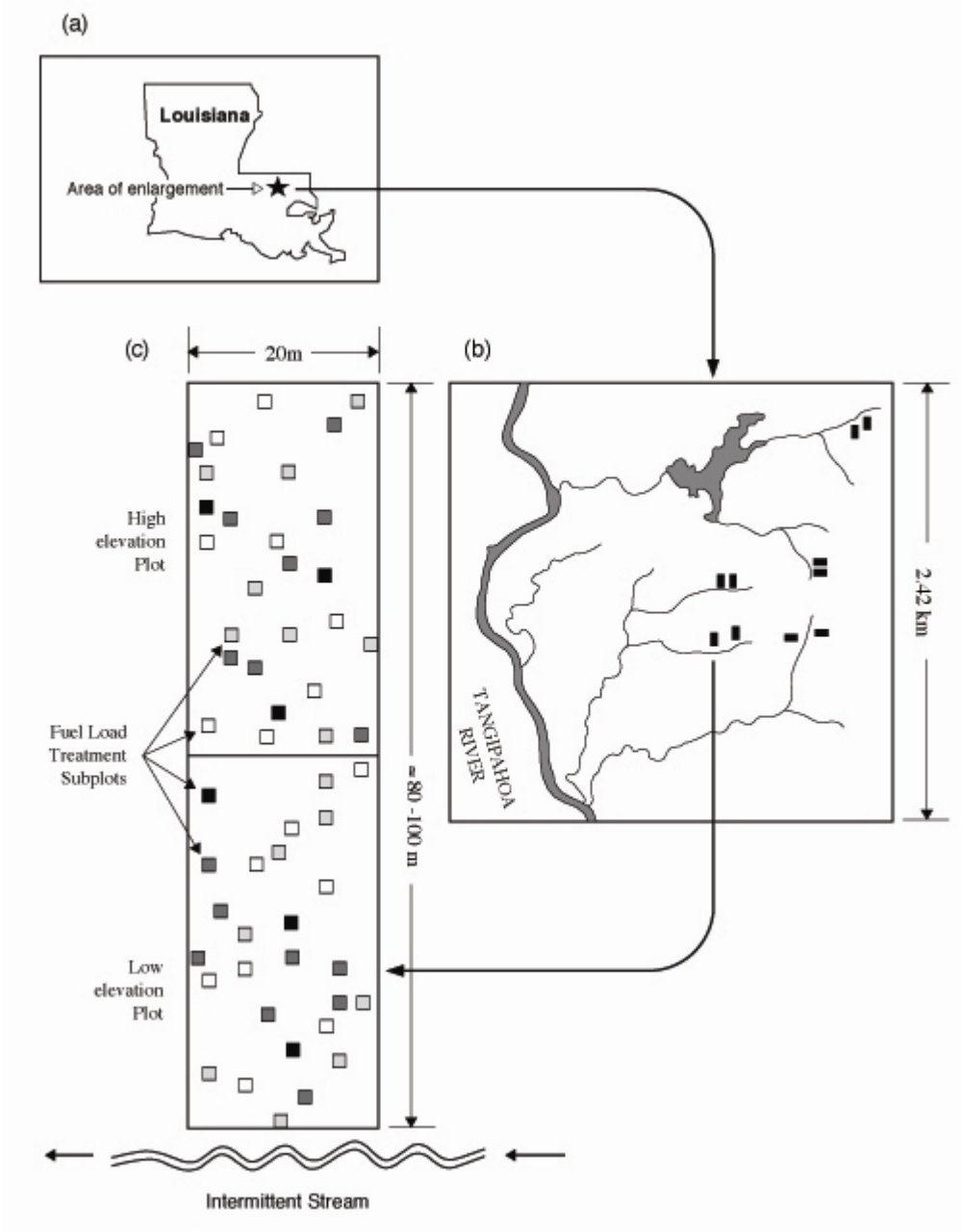


Figure 2.1 Study site and layout of plots. **(a)** The location of Camp Whispering Pines in Louisiana. **(b)** Location of transects along ravines at CWP. **(c)** The division of transects into high and low elevation plots containing nested fuel load subplots. Differences in shading indicate treatments randomly assigned to subplots.

Elephantopus tomentosus), and both native *(*e.g., *Rhus copallinum, Gaylussacia dumosa, Ilex glabra, Vaccinium sp.)* and exotic shrubs (e.g., *Ligustrum sinense, Triadica sebifera,*).

CWP has been managed with biennial early growing season prescribed fires (April-May) since 1994. Fires are conducted one to several days after rains, usually with moderate winds. Blacklining around roads and human structures (Girl Scout tent units) is carried out in the morning of a prescribed burn. Once perimeters are secured (usually mid-morning), headfires are ignited and allowed to burn across the burn units unimpeded. Thus, fire behavior simulates a natural fire moving across the landscape, burning up and down slopes, as well as into ravines, depending on weather and fuel conditions.

Field Study

A total of 540 $1m^2$ subplots were used in the study. Two permanent transects were randomly located within each of five ravines at CWP in the summer of 1998; each ravine was associated with a different intermittent stream (Figure 2.1b). Each transect was oriented perpendicular to the stream channel and was 20 m wide, but varied in length (approx. 80-100 m) depending on the distance from bottom to top of the ravine. Changes in elevation along transects averaged 4.4m, ranging from 2.5 m to 6.4 m. Each transect was divided into a high (H) and low (L) plot based on the midpoints of the elevation ranges. Within each of the 20 plots, 27 $1m^2$ subplots, each containing at least one live shrub stem, were randomly located and permanently marked (Figure 2.1c). Defining plot limits on the basis of elevation resulted in different plot sizes within some transects. High and low plots covered approximately the same area within 5 of 10 transects, but in the remaining 5, high elevation plots tended to be about 20% larger. Since all sampling took place within $1m^2$ subplots and all plots contained

the same number of subplots, the bias in plot area was ignored. Furthermore, smaller plot size at low elevation did not affect the distance between randomly placed subplots.

Fuel load treatments: Fuel treatments were designed to mimic natural variation in fuel loads in longleaf pine savannas. I randomly applied one of 4 different fuel load treatments to each $1m^2$ subplot no more than 2 weeks prior to experimental fires in 1999 and 2001. Pine needle addition and wood addition treatments mimicked the input of needles or coarse woody debris by a tree-fall or branch-fall within a frequently burned savanna. Pine needle addition treatments were applied by covering each subplot and a 30 cm buffer zone with a layer of longleaf pine needles approximately 10 cm deep. Wood addition consisted of adding pine wood pieces (each approximately 2 cm diameter, 1 m length) across the subplot. In 1999, wood addition treatments consisted of equal parts longleaf pine and loblolly pine wood, but in 2001 only longleaf pine wood was used. Fine fuel removal treatments mimicked decreases in fuels that occur in areas near animal burrows or away from large pines. I removed all pine needles, some dead grasses and litter from each subplot, as well as a 30 cm buffer zone. Controls were unaltered fuels.

Immediately before fires, I sampled pre-fire fuel loads for two purposes. First, samples from unaltered control subplots were used to quantify the range of naturally occurring fuel load densities in frequently burned pine savanna. Second, pre-fire samples from treated subplots provided a measure of the effect of treatment on the density of available fuel. Pre-fire samples consisted of all aboveground biomass (both live and dead) from ground level to 1 m height, collected from a small area within the 30 cm treated buffer zone around each subplot . During 1999, 30 x 30 cm fuel samples were collected adjacent to all fuel load treatment subplots. In 2001, 20 x 20 cm fuel samples were collected adjacent to half of the

fuel load treatment subplots. Samples were oven dried at 50ºC, sorted into fuel type categories and weighed. Fuel samples were separated into four categories: 1) dead fine fuels, 2) live fine fuels, 3) dead wood and 4) live wood. Dead fine fuels include pine needles, dead grasses, leaves and other litter. Dead wood included downed pine branches, pine cones, pine bark, and standing dead shrubs. Live fine fuels included grasses and forbs, and live wood fuels included stems and leaves of shrubs.

Fuel load treatments altered the amount and type of fuels (Figure 2.2a). Pine needle additions generated fuel biomass that averaged > 2 kg/m^2, about twice that of unaltered controls (~1kg/m^2). Total fuel biomass averaged >5 kg/m^2 in wood addition plots, about five times as much as that in the control plots; wood was added to the existing fuel biomass present. Conversely, fuel removal subplots averaged 0.2 kg/m^2, less than half the fine fuel biomass of controls. Average fuel density was 2.17 kg/m^2 in 1999 and 2.29 kg/m^2 in 2001; the increase was statistically significant (ANOVA $p=0.0025$). Fuel density within control subplots did not change significantly from 1999 to 2001. Thus it appeared that the overall increase in fuel density was not related to productivity but instead to differences in wood addition treatments. Resinous longleaf pine wood has higher specific gravity than loblolly pine wood, so the use of all longleaf pine wood in 2001 appears to account for this increase. The range of fuel densities produced by treatments captured the variation naturally occurring in unaltered subplots (Figure 2.2b).

Fires and post-fire data collection: The transects at CWP were burned by CWP staff in spring, 1999 and 2001. All plots and subplots were burned by either head or flanking fires during both years. In both years, plots and subplots within the same ravine were burned on the same day, but not all ravines were burned on the same day. Three different fires on three

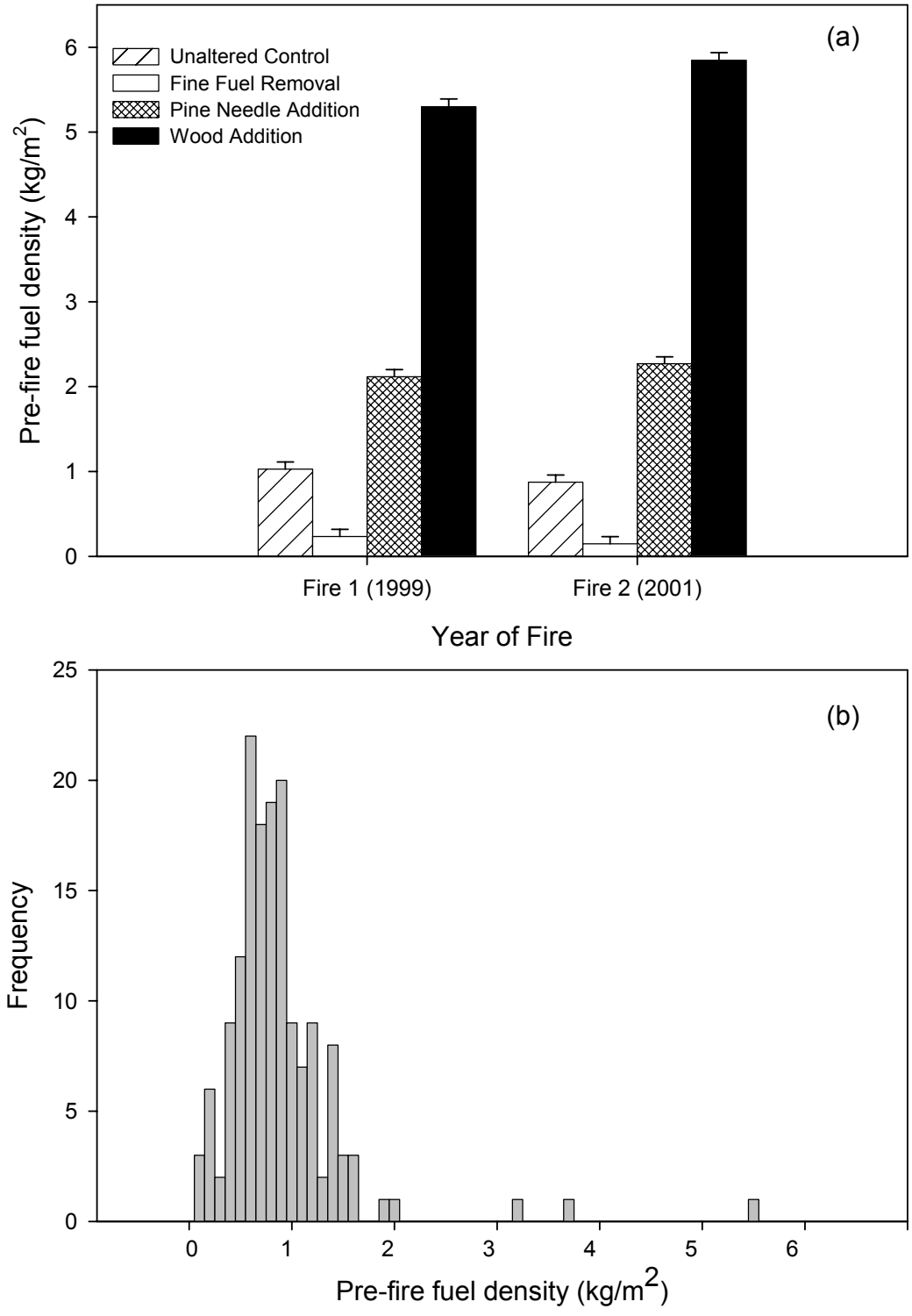


Figure 2.2 (a) Pre-fire fuel load density for early growing season (April) fires in 1999 and 2001. Values are the mean $\pm$ SE of biomass (kg/m^2) from ground level to 1 m height in unaltered control, fine fuel removal, pine needle addition and wood addition fuel load treatment subplots. **(b)** Frequency distribution of fuel density in unaltered controls prior 1999 fire.

different days were required to burn all ravines in the study in each year. Prescribed burning of study plots was conducted between April 14 and April 26 in 1999, and between April 11 and April 18 in 2001. Fires were ignited from one to 12 days following the last measurable rainfall. Rainfall patterns prior to fires differed between years. The average rain-free interval prior to fires was 8 days in 1999, almost twice that of 2001 (4.5 days). Similarly, total rainfall during the 6 weeks prior to burning was about 35% higher in 2001 (29.2 cm) than 1999 (18.7 cm).

Post-fire fuel samples were collected adjacent to both the treatment subplot and the pre-fire fuel sample. Post-fire fuel samples were oven dried at 50ºC, sorted into fine and wood fuels, and weighed. The difference between pre- and post-fire fuel samples was used to estimate percent consumption and the mass of fuel consumed. Fuel consumption was multiplied by low heat of combustion (*see* Wade and Johansen 1986, Johnson 1992) to calculate heat output per unit area. A low heat value of 18,572 kJ/kg, based on published values for fuel types from southeastern pine forests (Hough and Albini 1978), was used in all calculations. This value is the average for fine fuels composed of longleaf pine needles and twigs, as well as both live and dead herbaceous plant material.

Maximum fire temperatures at ground level were estimated in fuel load treatment subplots during both sets of fires. I used 15 different Tempil temperature indicating pellets (Big Three Industries, Inc., Tempilº Division, South Plainfield, New Jersey, USA) spanning a range of melting temperatures (48º, 132º, 212º, 302º, 371º, 454º, 538º, 621º, 704º, 843º, 954º, 1038º, 1149º, 1232º, 1288º, and 1371ºC) and individually wrapped in heavy-duty aluminum foil. On the morning before prescribed fires, a set of pellets was strung on wires and placed at ground level in each subplot. All pellets were recovered immediately after fires and scored

for melting. Melting temperatures were corrected for wrapping in aluminum foil using the regression equation of Drewa et. al. (2002). Adjusted melting temperatures for the 15 different pellets were: 85º, 189º, 289º, 400º, 486º, 589º, 693º, 796º, 899º, 933º, 1071º, 1209º, 1313º, 1450º, and 1553ºC, respectively.

The effect of fire on live aboveground shrubs was measured as the damage of leaves and stems. Less than 2 weeks after each fire, each $1m^2$ subplot was categorized by the amount of leaf and stem damage to shrubs that were < 2 m but > 30 cm height prior to fires. Each subplot was first classified as either "damage" or "no damage" due to the presence or absence of shrub crowns with visible damage to leaves. Visible leaf damage was defined as >10% of pre-fire leaves consumed or charred during fire. For "damage" subplots, a second categorization was made to provide an estimate of the severity of visible damage. Subplots containing shrubs with >90% consumption of leaves were considered to have sustained "complete" damage, while plots with visible consumption of <90% represented "partial" damage. The same categories were used to classify each subplot independently on the basis of stem damage. Stem damage was defined as visible consumption of either the main stem or primary branches.

Statistical Analyses

The experimental design was a repeated measures split-plot with blocks. Fuel consumption, fire temperature and shrub damage were measured in subplots that received fuel load treatments (split-plots) in each of two years (split-split-plots). Subplots were nested within plots(whole plots) located at low or high elevation. Elevation plots were nested within transects (sub-blocks) within ravines (blocks). Linear mixed models were constructed with

fuel, elevation and year as fixed effects, and subplots, plots, transects and ravines as random effects.

Treatment effects on fuel consumption and fire temperature were analyzed using ANOVA in PROC MIXED (SAS Institute 1997) . Replication of fuel load treatments was unbalanced, so a Satterthwaite approximation was used to calculate the most appropriate denominator degrees of freedom for F-tests. Orthogonal linear contrasts were constructed to test *a priori* hypotheses regarding fuel load treatment effects. The initial hypothesis tested was that subplots receiving fuel load treatments differed from subplots with unaltered fuels. The second hypothesis was that subplots where fuels were removed differed from subplots that received some type of fuel load addition. The third hypothesis was that subplots receiving pine needle addition differed from subplots receiving addition of wood. Other differences between specific treatment combinations were examined as *post hoc* analyses with Tukey-Kramer pair-wise comparisons of least squares means.

Shrub damage data were analyzed using a generalized linear mixed model with a logit link. The appropriate model was generated by invoking PROC MIXED within the GLIMMIX macro (Littell et al. 1996). Damage categorizations were considered to consist of two sets of binomial responses (success=1, failure=0). First all subplots were used to determine the probability of occurrence of at least partial leaf or stem consumption. For this analysis, "damage" was considered to be success (=1), while "no damage" was failure (=0). Next the probability of complete damage was analyzed in subplots where at least some damage occurred. For this analysis, "complete" subplots were successes (=1) and "partial" subplots were failures (=0). "No damage" subplots were excluded from the second analysis. Since two analyses were run on the same data a Bonferroni correction was made on all p-

values for shrub damage data. For these, $\alpha = 0.05/2 = 0.025$ was used as the level of significance. As for fuel consumption and temperature data, orthogonal linear contrasts were constructed to test *a priori* hypotheses regarding fuel load treatment effects on shrub leaf and stem damage. Other differences between specific treatment combinations were examined as *post hoc* analyses with Tukey-Kramer pairwise comparisons of least squares means. All models converged to analytical solutions in < 20 iterations.

Results

Effects of Treatments on Indicators of Fire Intensity: Fuel Consumption, Heat Output, Maximum Temperature

Both fires produced local variation in fire intensity. Heat output per unit area ranged from < 1000 kJ/kg to >80,000 kJ/kg among subplots within the same plots during single fires. Ambient temperature at ground level was elevated to at least 85ºC in all subplots where fire temperatures were recorded, and maximum temperatures reached >1000ºC in some subplots. As a result, differences of several hundred degrees occurred among subplots within plots. The flame front passed through all 10 transects in each year; measurable fuel consumption occurred in all subplots where pre- and post-fire fuel samples were collected.

Fuel effects: Fuel load treatments affected percent fuel consumption (Figure 2.3a; Table 2.1). Overall fuel consumption was greatest (88%) in pine needle addition subplots and least (30%) in fuel removal subplots. Linear contrasts of differences among fuel load treatments indicated that percent fuel consumption in treated subplots differed from that of unaltered controls (contrast $p=0.003$). Among treated subplots, percent fuel consumption in fine fuel removal subplots was significantly lower (contrast $p<0.001$) than in subplots where either pine needles or wood had been added. Furthermore, percent fuel consumption was

Figure 2.3 The effects of fuel load treatments on indicators of fire intensity, pooled over all fires. **(a)** Percent fuel consumption (LS means $\pm$ 95% CI) within unaltered control, fine fuel removal, pine needle addition, and wood addition fuel load treatments. Percent fuel consumption was calculated as the percent difference in mass of pre-fire fuel samples and adjacent post-fire fuel samples collected during the first week following fires. **(b)** Heat output per unit area (LS means $\pm$ 95% CI) among fuel load treatments. Heat output per unit area is calculated by multiplying the total amount of fuel consumed by the low heat of combustion for fuels of a particular type. A low heat value of 18,572 kJ/kg (Hough and Albini 1969) was used for all calculations in this study. **(c)** Maximum fire temperature (LS means $\pm$ 95% CI) at ground level.

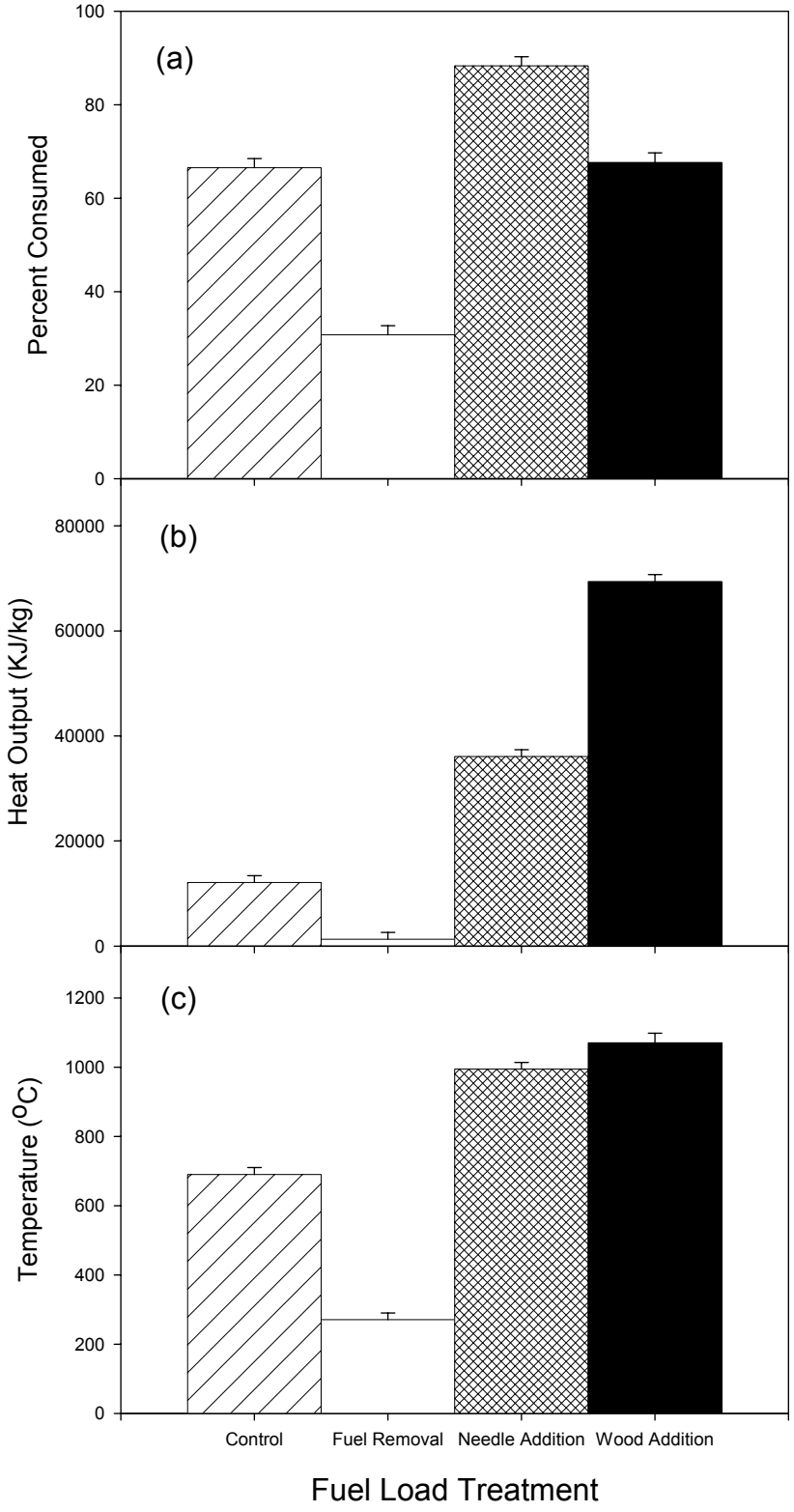

(a)
Percent Consumed
100
80
60
40
20
0
(b)
Heat Output (KJ/kg)
80000
60000
40000
20000
0
(c)
Temperature (°C)
1200
1000
800
600
400
200
0
Control
Fuel Removal
Needle Addition
Wood Addition
Fuel Load Treatment

Table 2.1 Results of mixed model ANOVA of percent fuel consumption. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	9.25	2.01	0.1891	
Fuel	3	261	355.1	<0.0001	*
Elevation x Fuel	3	261	0.49	0.6911	
Year	1	278	219.77	<0.0001	*
Elevation x Year	1	278	1.13	0.28814	
Fuel x Year	3	278	32.76	<0.0001	*
Elevation x Fuel x Year	3	278	0.79	0.4991	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	261	8.59	0.0037	*
Removal x (Needle Addition + Wood Addition)	1	261	877.6	<0.0001	*
Needle Addition x Wood Addition	1	260	117.6	<0.0001	*

significantly higher in pine needle addition subplots than in wood addition subplots (contrast $p<0.001$).

Differences in fuel consumption among fuel load treatments resulted in very large differences in heat output per unit area (Figure 2.3b; Table 2.2). Overall heat output in wood addition plots (69,433 KJ/kg) was nearly twice that of pine needle addition plots (36,073 KJ/kg) and almost six times that of unaltered controls (12,092 KJ/kg). Heat output of fine fuel removals (1,288 KJ/kg) was an order of magnitude lower than that of unaltered controls. All tests of *a priori* hypotheses of differences among treatments were significant ($p<0.001$ for all contrasts).

The effects of fuel load treatments on maximum fire temperatures were similar to those of fuel consumption and heat output per unit area (Figure 2.3c; Table 2.3). Pine needle addition and wood addition produced the hottest fires (average maximum temperatures > 1000ºC). These fire temperatures were 300ºC higher than unaltered controls and 700ºC higher than that of fine fuel removals. All differences among fuel load treatments were significant (Table 2.3).

Year effects and year by fuel interactions: Percent fuel consumption tended to be lower in 2001 than in 1999. Overall percent fuel consumption was 72% in 1999 fires and 56% in 2001 fires; these differences were significant ($p<0.001$; Table 2.1). Among fuel load treatments, consumption in unaltered controls, fine fuel removals and wood addition treatments was lower in 2001 than in 1999. The decrease was particularly evident for fine fuel removal and wood addition treatments (Figure 2.4a). Consumption in fine fuel removal subplots decreased from 41% in 1999 to 21% in 2001. Among wood addition subplots consumption decreased from 85% in 1999, comparable to pine needle addition subplots in

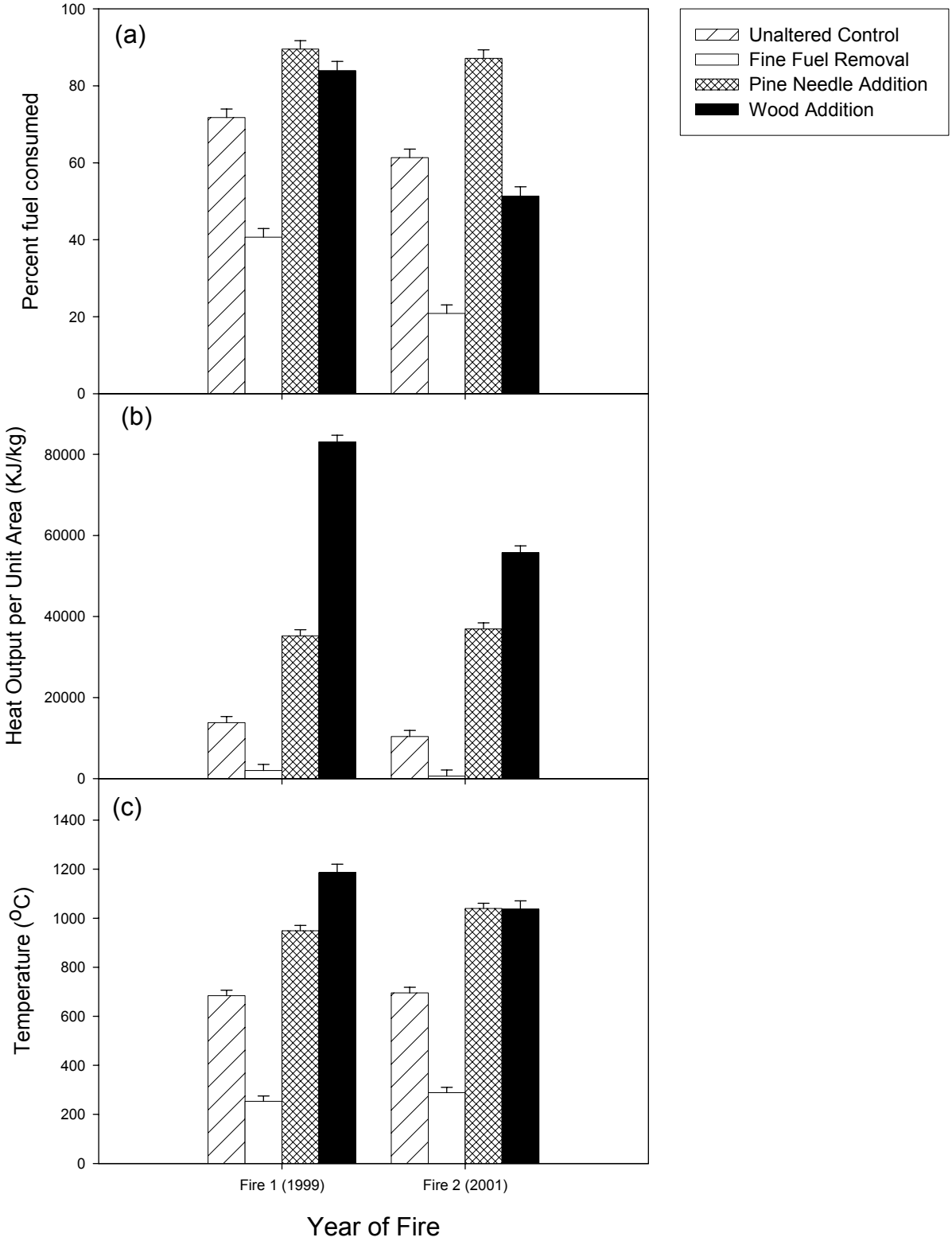
Table 2.2 Results of mixed model ANOVA on heat output per unit area. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	9.2	1.26	0.2912	
Fuel	3	269	1202.75	<0.0001	*
Elevation x Fuel	3	269	1.69	0.169	
Year	1	278	85.18	<0.0001	*
Elevation x Year	1	278	1.97	0.1611	
Fuel x Year	3	278	57.54	<0.0001	*
Elevation x Fuel x Year	3	278	1.35	0.2578	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	269	632.62	<0.0001	*
Removal x (Needle Addition + Wood Addition)	1	269	2563.43	<0.0001	*
Needle Addition x Wood Addition	1	269	752.01	<0.0001	*

Table 2.3 Results of mixed model ANOVA on maximum fire temperature. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	8	0.25	0.629	
Fuel	3	396	811.15	<0.0001	*
Elevation x Fuel	3	396	2.79	0.046	*
Year	1	412	1.36	0.244	
Elevation x Year	1	412	0.06	0.809	
Fuel x Year	3	412	4.22	0.006	*
Elevation x Fuel x Year	3	412	0.91	0.4373	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	396	45.95	<0.0001	*
Removal x (Needle Addition + Wood Addition)	1	396	2232.2	<0.0001	*
Needle Addition x Wood Addition	1	396	22.99	0.002	*

Figure 2.4 The effects of fuel load treatments on indicators of fire intensity within fires in 1999 and 2001. **(a)** Percent fuel consumption, **(b)** Heat output per unit area, and **(c)** Maximum fire temperature are calculated as indicated in Figure 2.3. Note the interaction of fuel by year resulting from the decrease in intensity of wood addition treatments in 2001.


(a)
(b)
(c)
Percent fuel consumed
Heat Output per Unit Area (KJ/kg)
Temperature (°C)
Unaltered Control
Fine Fuel Removal
Pine Needle Addition
Wood Addition
Fire 1 (1999)
Fire 2 (2001)
Year of Fire

that year, to 49% in 2001, less than unaltered controls in that year. These decreases in percent consumption resulted in a significant fuel by year interaction ($p<0.001$).

Heat output per unit area also differed between fires in different years (Figure 2.4b). Average overall heat output was 23% lower in 2001 fires; this difference was significant ($p<0.001$; Table 2.2). The decrease was primarily a result of the 32% lowered heat output of wood addition treatments in 2001 (Figure 2.4b). Although heat output of wood addition treatments decreased significantly over the two years (Tukey-Kramer $p<0.0001$), their heat output remained higher than that of any other fuel load treatment. No other fuel load treatments differed significantly between the two years. These differences resulted in a significant fuel by year interaction ($p<0.0001$).

Unlike fuel consumption and heat output, overall maximum fire temperatures did not differ between years ($p=0.244$; Table 2.3). Nonetheless, there was a significant interaction of fuel by year ($p=0.006$). Differences in temperatures in pine needle addition plots appeared to produce the significant interaction (Figure 2.4c). Temperatures in pine needle addition plots increased 90ºC from 1999 to 2001 (Tukey-Kramer $p=0.013$). No significant differences in maximum temperatures occurred in wood addition subplots in the two different fires, as occurred for fuel consumption and heat output.

Elevation effects and elevation by fuel interactions: Elevation had little effect on fire intensity. Mean percent fuel consumption pooled over all fuel load treatments was 63% in low elevation plots and 65% in high elevation plots ($p=0.19$), resulting in similar average heat output values between low elevation (29,254 kJ/kg) and high elevation (30,189 kJ/kg) plots ($p=0.26$). Similarly, maximum fire temperatures averaged 760ºC at low elevations and 774ºC at high elevations; these differences were not significant ($p=0.629$). An elevation by fuel

treatment interaction for maximum fire temperature approached significance (p=0.05). Pine needle addition subplots increased slightly (≈50ºC) from low to high elevation plots, while fuel removal and control subplots decreased ≈ 40ºC.

Effects of Treatments on the Probability of Damage to Vegetation: Consumption of Shrub Leaves and Stems

Fuel effects: Visible leaf damage occurred in almost all subplots, but there were differences in the probability of damage among fuel load treatments. The probability of visible damage to leaves was >0.9 for unaltered controls, pine needle additions and wood addition subplots, but only 0.7 for fuel removal subplots (Figure 2.5a). The overall effect of fuel load was significant ($p<0.0001$, Table 2.4). Linear contrasts indicated this resulted from significantly decreased leaf damage in fuel removal subplots relative to subplots that received either pine needle or wood addition (contrast $p<0.0001$) or unaltered controls (Tukey-Kramer $p<0.0001$).

Among subplots where visible leaf damage occurred, there was a nearly 0.8 probability that this damage was complete, but this probability differed among fuel load treatments (Figure 2.5b). Probability of complete damage was greater among pine needle addition ($\pi=0.94$) and wood addition ($\pi=0.90$) subplots than in unaltered controls ($\pi=0.77$). The probability of complete damage was lowest in fine fuel removal subplots ($\pi=0.43$). The overall effect of fuel load treatment was highly significant ($p<0.0001$, Table 2.5). The probability of complete leaf damage in fine fuel removals differed significantly from that of fuel addition treatments (contrast $p<0.0001$) as well as unaltered controls (Tukey-Kramer $p<0.0001$). Furthermore, unaltered controls differed significantly from pine needle additions (Tukey-Kramer $p<0.0001$) but only marginally from wood additions ($p=0.06$). There was no

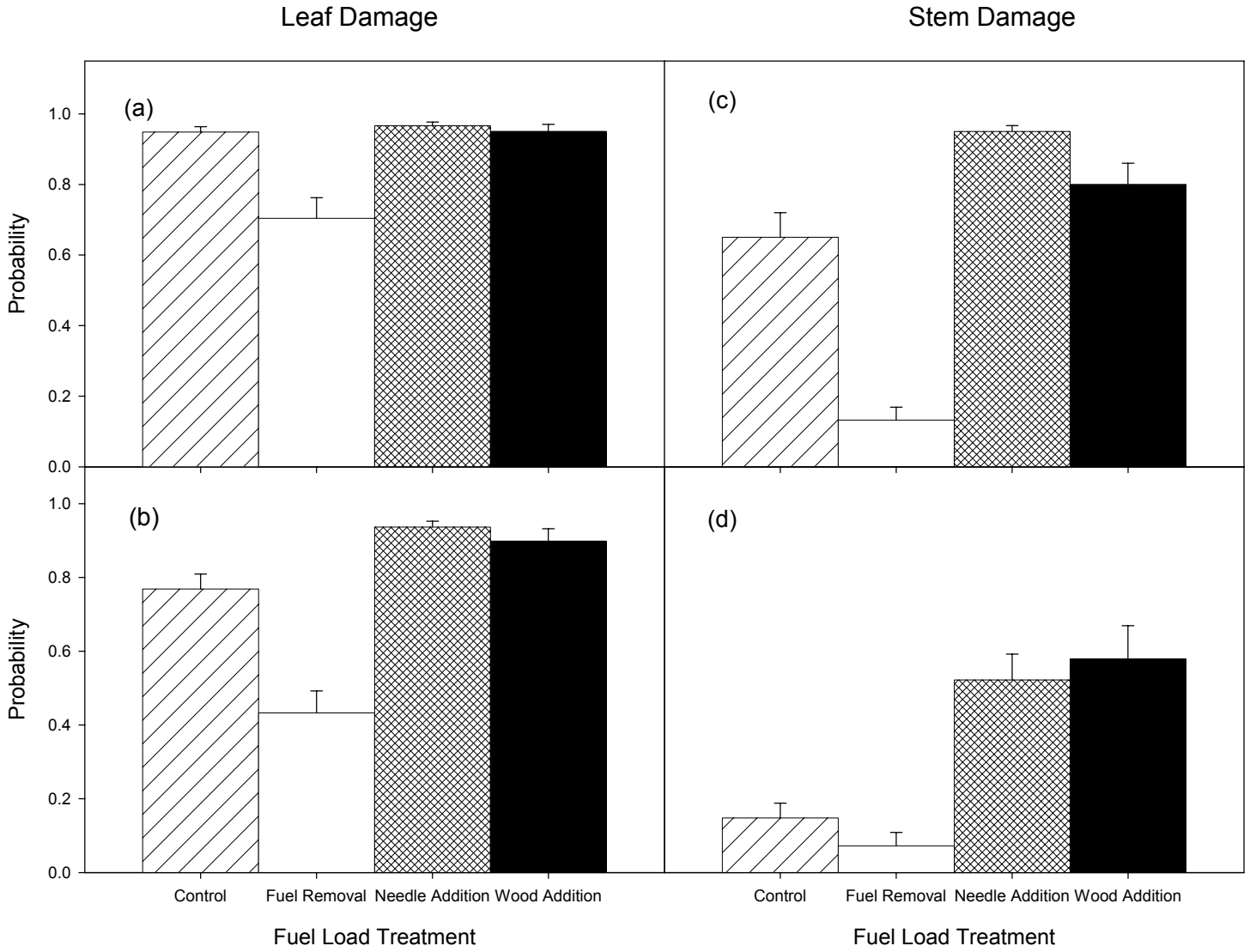


Figure 2.5 Probability of leaf and stem damage among fuel load treatment subplots. Data are pooled over years and elevation. Values are LS means ± SE of probabilities back-transformed from logits. **(a)** Probability of visible damage (>10% consumed) to shrub leaves. **(b)** Probability of complete damage (>90% consumed) to shrub leaves. **(c)** Probability of visible damage (>10% consumed) to shrub stems. **(d)** Probability of complete damage (>90% consumed) to shrub stems.

Table 2.4 Results of generalized linear mixed model analysis of probability of visible damage to shrub leaves. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Significance level is p<0.025.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	10.1	7.36	0.02	*
Fuel	3	594	30.69	<0.0001	*
Elevation x Fuel	3	596	1.63	0.1819	
Year	1	684	0.24	0.6447	
Elevation x Year	1	684	3.09	0.0794	
Fuel x Year	3	686	12.46	<0.0001	*
Elevation x Fuel x Year	3	686	1.35	0.2586	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	637	3.64	0.0568	
Removal x (Needle Addition + Wood Addition)	1	533	64.43	<0.0001	*
Needle Addition x Wood Addition	1	674	0.84	0.3601	

Table 2.5 Results of generalized linear mixed model analysis of probability of complete damage to shrub leaves. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Significance level is p<0.025

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	9.25	5.98	0.037	*
Fuel	3	516	33.42	<0.0001	*
Elevation x Fuel	3	512	1.17	0.32	
Year	1	483	14.93	0.0001	*
Elevation x Year	1	484	2.92	0.088	
Fuel x Year	3	496	3.09	0.0267	
Elevation x Fuel x Year	3	496	6.54	0.0002	*
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	464	1.92	0.1665	
Removal x (Needle Addition + Wood Addition)	1	512	87.02	<0.0001	*
Needle Addition x Wood Addition	1	626	1.46	0.2269	

significant difference in complete damage probability between pine needle and wood fuel addition treatments (contrast p=0.2269).

The overall probability of visible damage to shrub stems was > 0.5 in all fires, but this probability was strongly affected by fuel load treatments. Similar to the pattern for leaf damage, the probability of damage was highest in pine needle addition subplots and lowest in fuel removals. The probability of damage in pine needle addition subplots was 15% more than in wood addition subplots, 30% more than that of unaltered fuels and more than 7 times that of fuel removals (Figure 2.5c). The overall effect of fuel treatment was significant ($p<0.0001$, Table 2.6), as were all linear contrasts and pair-wise comparisons of treatment differences.

Complete shrub damage was relatively infrequent, with an overall probability of <0.3. Among pine needle addition and wood addition subplots, the probability of complete damage was >0.5, more than 3 times higher than in unaltered controls (π=0.15) and more than 7 times higher than fine fuel removals (π=0.07, Figure 2.5d). The overall effect of fuel load treatments was highly significant ($p<0.0001$, Table 2.7), as were linear contrasts of treated subplots compared to unaltered controls (p=0.0012), and fuel removals compared to fuel additions ($p<0.0001$). However, effects of pine needle additions did not differ significantly from wood additions (p=0.5275), nor did unaltered controls differ from fuel removals (Tukey-Kramer p=0.48).

Year Effects and Year by Fuel Interactions: Fires in different years varied in their effects on shrub leaf damage. Although the overall probability of leaf damage was approximately 0.5 in both years, the probability of damage among fine fuel removal subplots decreased by 32% from 1999 to 2001. This resulted in a significant fuel by year interaction

Table 2.6 Results of generalized linear mixed model analysis of probability of visible damage to shrub stems. Error term for Elevation = Elevation x Transect (Ravine). Error term for Fuel and interactions = Subplot (Fuel x Elevation x Transect (Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Significance level is p<0.025

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	13	9.16	0.0097	*
Fuel	3	526	106.69	<0.0001	*
Elevation x Fuel	3	524	0.85	0.4685	
Year	1	625	13.38	0.0003	*
Elevation x Year	1	625	1.33	0.2501	
Fuel x Year	3	625	0.39	0.7595	
Elevation x Fuel x Year	3	626	0.26	0.855	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	434	1.03	0.3114	
Removal x (Needle Addition + Wood Addition)	1	588	276.93	<0.0001	*
Needle Addition x Wood Addition	1	612	20.5	<0.0001	*

Table 2.7 Results of generalized linear mixed model analysis of probability of complete damage to shrub stems. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Significance level is p<0.025

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	12.5	4.71	0.0581	
Fuel	3	412	19.86	<0.0001	*
Elevation x Fuel	3	408	0.55	0.6485	
Year	1	490	0.17	0.6801	
Elevation x Year	1	487	0.03	0.8575	
Fuel x Year	3	392	4.36	0.0049	*
Elevation x Fuel x Year	3	391	0.18	0.9129	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	466	10.62	0.0012	*
Removal x (Needle Addition + Wood Addition)	1	576	26.4	<0.0001	*
Needle Addition x Wood Addition	1	280	0.4	0.5275	

($p<0.0001$), although the overall year effect was not significant ($p=0.64$). The overall probability of complete damage to leaves was 13% higher in 1999 fires than 2001 fires, resulting in a significant year effect ($p=0.001$).

The probability of stem damage was affected by the year in which fires occurred. The probability of visible stem damage was 0.74 in 1999 and decreased to 0.61 in 2001. This difference was significant ($p=0.0003$). The probability of complete stem damage was also affected by year, but not in a consistent manner across fuel load treatments. The complete damage probability for unaltered fuels and needle additions increased, while the probability for wood addition and fuel removals decreased. This resulted in a significant year by fuel interaction ($p=0.0049$).

Elevation effects: Unlike fire intensity, damage probabilities tended to be affected by elevation along a topographic gradient. The probability of leaf damage was 0.9 in low elevation plots and was only slightly higher in high elevation plots ($\pi=0.947$), but this difference was significant ($p=0.02$). Similarly, the probability of complete leaf damage was 0.76 in low elevation plots and 0.85 in high elevation plots. This difference approached significance ($p=0.04$). Elevation differences were consistent across fuel load treatments, as no elevation by fuel interactions were significant. However, the three way interaction of elevation, fuel and year was significant ($p=0.0002$).

Stem damage probabilities were less affected by elevation. The probability of stem damage in high elevation plots was 0.75, 20% higher than that of low elevation plots ($p=0.0097$). However the probability of complete damage did not differ significantly between high and low elevation plots ($p=0.0641$).

Discussion

Variation in the amounts and type of fuels strongly influences fire intensity at small scales within single fires in frequently burned plant communities. In this study, variation in fuel loads at a scale as small as $1m^2$ and within the range of naturally occurring fuel densities produced significant local variation in fire intensity. The addition of either pine needles or woody fuels consistently produced local "hotspots" where maximum temperature and heat output were as much as an order of magnitude higher than that of nearby unaltered fuels. Conversely, fine fuel removal produced areas where elevated temperatures and fuel combustion were minimal during fires. Prior studies in pine savannas have also related high fire temperatures to areas of high needle density, which tend to occur naturally near canopy pines (Williamson and Black 1981, Platt et al. 1991, Grace and Platt 1995). Experimental studies in Mediterranean-type ecosystems (Moreno and Oechel 1991, Molina and Llinares 2001) and tropical dry forest (Kennard et al. 2002) have shown similar positive effects of primarily woody fuel additions on fire intensity. Kennard et al. (2002) also removed fuels and recorded maximum fire temperatures several hundred degrees lower than for fuel addition treatments. None of the previous experimental studies have linked the amounts of fuel added or removed to naturally occurring fuel loads in the study system.

Differences in fuel moisture may interact with fuel loads to produce variation in fire intensity among fires in different years. In this study, overall percent fuel consumption tended to be lower in 2001 than in 1999, although overall pre-fire fuel loads were slightly higher. Average rain-free intervals prior to fires in 1999 were nearly twice that of 2001. Fuel moisture is an important determinant of fuel consumption and fire behavior (Pyne et al. 1996, Nelson 2001); shorter rain-free intervals may have resulted in wetter fuels and reduced

consumption in 2001. Furthermore, percent fuel consumption was particularly reduced (~50%) in wood addition and fuel removal treatments. Differences in consumption of woody fuels may have resulted from longer drying times of coarse woody fuels compared to fine fuels (Pyne et al. 1996, Nelson 2001). In areas where fine fuels had been removed, fuel continuity was reduced; thus fires in wetter fuels were more likely to be patchy and of lower intensity (Slocum et al. 2003). These results suggest that although variable intensity within single fires may be almost completely a function of fuel loads, weather conditions preceding fires are likely to influence relationships between fuel loads and fire intensity

Pre-fire weather conditions did not affect maximum fire temperatures to the same extent as fuel consumption or heat output. Fire temperatures in unaltered fuels, fine fuel removals, and wood addition did not decrease significantly from 1999 to 2001, while temperatures in pine needle addition subplots significantly increased. These results suggest that in dry years like 1999, fuel consumption, heat output and maximum temperature are similar indicators of fire intensity, while in wetter years like 2001 maximum fire temperatures may overestimate the amount of heat being produced by fires. Molina and Llinares (2001) doubled fuel loads in Mediterranean maquis vegetation and found that heat output doubled while maximum fire temperatures increased only by ~20%. Thus the effects of fuel load variation on fire intensity may be more completely described by measures of fuel consumption or heat output than maximum fire temperature.

Through its effects on fire intensity, fuel manipulation created variable patterns of damage to shrubs. With fuel addition the probability of damage to shrubs tended to increase, while damage decreased when fuels were removed. Similarly, Ansley et al. 1998 found that fire damage to leaves of mesquite in Texas savannas was positively correlated with fuel

availability. The ability to detect fire intensity effects may depend on the type of damage being evaluated. For example, the probability of damage to leaves was nearly 100% percent for unaltered fuels and both fuel addition treatments. Differences in the effects of these treatments were not apparent until the probability of more severe damage (complete leaf damage) was estimated. This indicated that fuel addition treatments produced significantly more severe leaf damage than did unaltered fuels. In contrast, differences in the probability of extreme damage (complete stem consumption) were not visible between unaltered controls and fine fuel removals. Thus quantifying the effects of variable fire intensity on plants may require investigating various types of damage.

Fuel consumption may be the most important fire characteristic for predicting damage to shrubs in pine savannas. The probability of shrub damage in all treatments tended to be lower in 2001 fires, paralleling decreases in fuel consumption and heat output. Since maximum temperature did not decrease from 1999 to 2001, this suggests that fuel consumption and heat output should be more important determinants of shrub damage. Nonetheless, the probability of damage in wood addition treatments was never significantly higher than that of pine needle addition treatments, although heat output in wood addition subplots was significantly higher. This suggests that the completeness of fuel consumption may provide the most reliable prediction of shrub damage. In some wood addition subplots, heat output was large as a result of the volume of fuel consumed, but consumption was patchy within subplots. Specifically, wood addition subplots had a tendency to burn more completely in the middle of the subplot than at the edges (J. Thaxton, *pers. obs.*). Thus heavy accumulations of woody fuel may not always result in complete shrub damage, particularly under moist conditions where consumption may be reduced.

Shrub damage across elevation gradients was not completely related to fire intensity. Although fire intensity did not differ between high and low elevation plots, shrub damage was less at low elevations. This may be because shrubs were larger lower on the slopes. Prior to fires in 1999, some shrubs, particularly *Ligustrum sinense*, in low elevation plots had not been top-killed by previous fires (W. Platt, *pers. obs.*). These shrubs were > 2 m height at the time of the first fire and were significantly larger than shrubs farther upslope. This may have accounted for a smaller proportion of leaves and stems being damaged or consumed at low elevations. Another possibility is that some fire characteristic (e.g., flame length) not measured in this study, is affected by elevation and also is important in producing patterns of damage. I quantified fire intensity only as a function of the magnitude and duration of heating near the soil surface. Visible damage to taller shrubs may be more related to flame height than surface heating (Morrison and Renwick 2000). This could account for patterns of damage along topographic gradients that are not predicted by fuel consumption or fire temperature.

Variation in fire intensity resulting from small-scale differences in fuels may be an important source of environmental heterogeneity in frequently burned pine savannas. High fire intensity and subsequent damage to shrubs may alter post-fire environments by decreasing the dominance of established individuals. In a previous study (Brewer et al. 1996), groundcover gaps generated by the experimental addition of large woody fuels persisted as areas largely absent of cover for at least 2 growing seasons. These areas of reduced cover of large established individuals may provide establishment opportunities for herbaceous species that re-grow quickly and produce widely dispersed seeds soon after fires. Furthermore, soil moisture, nutrients and topography affect species distributions, particularly of herbs, in

frequently burned pine savannas (Walker and Peet 1983, Drewa et al. 2002). Thus local heterogeneity produced by fire intensity may interact with other environmental factors to promote local species diversity by producing a range of post-fire microhabitats. In this way, a spatially variable recurrent non-catastrophic disturbance (Platt and Connell 2003) may be increasing the diversity of species that coexist in the groundcover of longleaf pine savannas.

CHAPTER 3

EFFECTS OF FIRE INTENSITY ON RESPROUTING OF GROUNDCOVER SHRUBS

Introduction

In plant communities that experience recurrent large disturbances, variation in the frequency, timing and intensity of disturbances may be a significant source of environmental and demographic heterogeneity. In fire-frequented communities, variation in the characteristics of individual fires may produce temporally and spatially heterogeneous environmental conditions that differentially affect the survival and reproduction of resident species (Williamson and Black 1981, Rebertus et al. 1989a, Turner et al. 1997). For example, fires in different seasons have been shown to differentially affect the survival and resprouting of both woody (Glitzenstein et al. 1995, Olson and Platt 1995, Drewa et al. 2002, Kennedy and Potgieter 2003) and herbaceous species (Brewer and Platt 1994b, a, Howe 1994) in savannas and grasslands. Thus a range of species that differ in their life histories can be expected in communities experiencing variable recurrent disturbances (Matlack and Good 1989, Rebertus et al. 1993, Howe 1994, Gignoux et al. 1997). This leads to the prediction that increasing the frequency of disturbances of a particular type may alter patterns of abundance and composition within a community (Hoffmann 1998, Menges and Hawkes 1998).

The effects of variable fire regimes on woody plants in savannas may be a function of both independent and interactive effects of fire regime components. Early growing season fires tend to produce higher mortality and reduced resprouting of trees and shrubs than do dormant season fires (Kauffman and Martin 1990, Platt et al. 1991, Waldrop et al. 1992, Glitzenstein et al. 1995, Olson and Platt 1995, Williams et al. 1998, Drewa et al. 2002). Two non-mutually exclusive hypotheses have been proposed to explain this pattern (Glitzenstein et al. 1995). The “tree physiology hypothesis” suggests that fire season effects are a result of fires occurring when the physiological or phenological status of plants makes them most

susceptible to fire effects. Conversely, the "ambient temperature" hypothesis suggests that fire intensity, independent of season or timing, is the most important determinant of fire effects. Growing season fires tend to be of higher intensity than fires in the dormant season (Kauffman and Martin 1990, Platt et al. 1991, Olson and Platt 1995, Drewa et al. 2002). No consistent pattern has emerged, however, among studies that have indirectly tested the "ambient temperature" hypothesis. Glitzenstein et al. (1995) found substantial effects of fire intensity on mortality of trees in longleaf pine savannas, while other studies have found limited evidence of fire intensity effects on groundcover shrub communities (Olson and Platt 1995, Drewa et al. 2002). No experimental studies have been conducted that include manipulation of fire intensity and measurement of its effects on community level patterns of mortality and resprouting of woody savanna species, although some studies have been conducted in other communities (Moreno and Oechel 1991, Drewa 2003).

Small-scale spatial variation in intensity of recurrent disturbances (such as fire) may be important to local patterns of plant population and community structure (Malanson 1984, Turner et al. 1997, Platt and Connell 2003). In communities that contain a continuous groundcover of potentially flammable vegetation (i.e. temperate grasslands, temperate and tropical savannas), fires are predictably frequent and often of low intensity (Andersen et al. 1998, Platt 1999, Ramos-Neto and Pivello 2000). Substantial spatial variation in fire intensity may occur, however, within single fires (Williamson and Black 1981, Gibson et al. 1990, Platt et al. 1991, Whight and Bradstock 1999). Local variation in intensity within a single fire is related to small-scale variation in fuels (Molina and Llinares 2001, Chapter 2), and may result in spatially variable effects on plants as well as heterogeneous post-fire environments. For example, in pine savannas of southeastern North America, fire temperature can be

elevated several hundred degrees in the vicinity of large canopy pines; these increased fire temperatures result in higher mortality of oaks near pines (Williamson and Black 1981, Platt et al. 1991). Thus spatial variation in fire intensity may alter survival and reproduction of established plants, as well as alter post-fire recruitment opportunities for species.

The response of resprouting woody vegetation to variation in fire intensity may be related to the morphology of underground resprouting organs. Following top-kill of aboveground plant parts, many woody species in fire-frequented communities resprout from dormant buds (Malanson and Trabaud 1988, Matlack et al. 1993b, Moreno and Oechel 1993, Olson and Platt 1995). In savannas for example, although almost all species are capable of some resprouting, species differ in the location and source of buds from which resprouts develop. Resprouts may develop from buds located on the root collar/crown (the point where the stem meets the root system), along lateral roots (root suckers) or from specialized underground structures such as lignotubers and rhizomes (Tiedemann et al. 1987, del Tredici 2001). While sprouting from the root collar is one of the most prevalent strategies in woody species, it constrains the location of sprouts to a point near the basal portion of the dead stem (del Tredici 2001). Furthermore, it means that the point of origin of the sprout is near the surface of the soil, potentially exposing it to elevated temperatures during fires (Drewa et al. 2002). In contrast, sprouts from rhizomes or root suckers are capable of being located significant distance from the parent stem, at varying depths belowground, and may result in clonal spread (Matlack et al. 1993a, b).

We conducted a five year experimental study of the effects of local variation in fire intensity on shrub community dynamics in a frequently burned longleaf pine savanna. I repeatedly manipulated the amount and type of fuels available to fires at small spatial scales

($1m^2$) within replicated plots across elevation gradients. With this experimental set-up, I was able to quantify the effects of fuels, elevation and time on resprouting, growth and mortality of the shrub community. Although previous studies in pine savanna groundcover shrub communities have tended to find only limited effects of fire intensity on shrub resprouting (Olson and Platt 1995, Drewa et al. 2002), neither of these studies directly manipulated fire intensity within single fires. By altering fuel loads within single growing season fires, I was able to control for interactive effects of fire frequency and season and provide a direct experimental test of the ambient temperature hypothesis. Furthermore I compared resprouting responses among groups of species that differed in the morphology of their underground resprouting organs. I tested the following hypotheses: 1) Small-scale variation in fire intensity, produced by small-scale fuel variation, predictably affects the overall number and size of shrub resprouts as well as the probability of genet mortality following fires. 2) The effects of fuels on shrubs differ across elevation gradients and different years. 3) Shrub response to fire intensity will be predictable on the basis of the mode of resprouting and the relative ability of species to colonize open space with new ramets. My study indicates that small-scale variation in a non-catastrophic disturbance such as fire may have significant effects on community composition and structure.

Methods

Study Site and History

Prior to European settlement, >90% of the land area of the coastal plain of the southeastern United States was covered by open savanna/woodlands with a discontinuous overstory composed almost entirely of longleaf pine (*Pinus palustris)* and a diverse groundcover of shrubs and herbs (Frost 1993, Platt 1999). Frequent low intensity ground fires

(occurring at more than once per decade; Platt et al. 1991) initiated by high frequencies of lightning strikes during the growing season were primarily responsible for maintenance of the open aspect of these habitats (Platt 1999). In the past 150 years, almost all pine savannas have disappeared as a result of deforestation and fire suppression. At present, <3% of the original area of pre-settlement pine savanna remains, with only 3,000 ha in old-growth stands (Frost 1993, Platt 1999). Most remaining pine savannas have experienced some history of altered fire regimes (fire suppression and/or dormant season burning) as well as increases in abundance of woody shrubs.

This study was conducted in upland longleaf pine savannas at Camp Whispering Pines, Tangipahoa Parish, in eastern Louisiana (30º41'N: 90º29'W; see Figure 2.1*)*. Pine savannas at Camp Whispering Pines (hereafter CWP) are located on well-drained Pleistocene aged sands capped by deposits of wind-blown loess. The terrain is moderately dissected with gentle (<8 %) slopes descending from ridge tops to the base of ravines along intermittent streams. The flora of CWP is characteristic of other frequently burned longleaf pine savannas on the Gulf Coastal plain. Longleaf pine (*Pinus palustris*) is the dominant canopy tree and the groundcover is a species diverse assemblage of grasses, shrubs and forbs. Groundcover species diversity at CWP is among the highest recorded in southeastern pine savannas (W.J. Platt, *unpublished data*)

Pine savannas at CWP were logged during the early 1930's, but bear no sign of plowing or extensive soil disruption. Canopy pines regenerated naturally following logging and many of the oldest trees are now >70 years old. For several decades following logging, open range grazing and frequent dormant season (November-February) fires occurred on the site. From the late 1970's to the late 1980's, all fires were suppressed. Since 1993, biennial

early growing season fires (April-May) have been conducted. Areas used in this study had received 3 growing season fires prior to the inception of the present study. Further information on the flora and history of CWP is available in Chapter 2 of this dissertation and Noel et al. (1998).

Field Study and Experimental Design

A multi-year study of shrub demography and fire effects was initiated at CWP in 1998. I randomly located two paired, permanent transects within each of five ravines associated with intermittent streams (see Figure 2.1b). Transects were oriented perpendicular to the stream channel, and were of fixed width (20 m) but variable length (approx. 80-100 m) to cover the entire distance from the ravine bottom to top. Each transect was divided into a high (H) and a low (L) plot based on the midpoints of the elevation ranges. Within each of the 20 plots, 27 $1m^2$ subplots, each containing at least on live shrub stem, were randomly located and permanently marked (see Figure 2.1c). This resulted in a total of 540 $1m^2$ subplots in the study.

To create local variation in fire intensity within prescribed fires, all subplots received one of four fuel load treatments immediately prior to each prescribed fire. Areas of locally increased fuels may occur in pine savannas as a result of needle-fall under large canopy pines (Williamson and Black 1981) or downed trees or branches following storms (Hermann 1993, Myers and van Lear 1998). Conversely, fine fuel may be reduced in the vicinity of animal burrows (Kaczor and Hartnett 1990) or around tip-mounds or other forms of soil disturbance (Hermann 1993). In this study, I mimicked this natural variation in fuels with the following treatments: pine needle addition, wood addition, fine fuel removal and unaltered control. For more information on the application of fuel load treatments see Chapter 2.

Fuel load treatments produced substantial variation in local fire intensity within experimental fires. All transects were burned by either head or flanking fires during the growing season (April) of 1999 and 2001. Large amounts of fuel and high fuel consumption in pine needle addition and wood addition subplots resulted in high levels of heat output and maximum fire temperatures in both fires. Maximum fire temperatures in pine needle addition and wood addition subplots consistently reached 1000ºC, while maximum temperatures averaged < 700ºC in controls and < 300ºC in fuel removal subplots. Heat output in wood addition subplots was nearly 70,000 kJ/kg, nearly twice that of pine needle addition subplots and six times that of controls. Fuel removal subplots produced an order of magnitude less heat than control subplots. For more information on fuel load treatment effects on fire intensity and damage to shrubs, refer to Chapter 2.

Shrub demography data were collected over five years. In an initial pre-fire census during the fall of 1998, all woody stems < 2 cm dbh in each subplot were counted and identified to species. From 1999-2002, all subplots were censused annually for shrub genet mortality, number of resprouts, and resprout size. All annual censuses were conducted in June; 2 months post-fire in 1999 and 2001 and 14 months post-fire in 2000 and 2002. Many shrub species in pine savannas are capable of clonal spread by resprouting along roots or rhizomes. Thus it was not possible to determine if individual ramets were of the same genets without excavating. For the purposes of this study, all the ramets of one species within a $1m^2$ subplots were considered to be one genet.

Statistical Analyses

The experimental design was a repeated measures split-plot with blocks. Fuel load treatments (split-plot factor) were randomly applied to subplots nested within high or low

elevation plots (whole plot factor). Elevation plots were located within transects (sub-block) nested within ravines (block). Dependent variables (shrub mortality, resprouting, height) were measured within subplots over four years (1999-2002, repeated factor). All linear mixed models were constructed with fuel, elevation and year as fixed effects, and subplots, transects and ravines as random effects. Replication of fuel load treatments was unbalanced, so in all analyses a Satterthwaite approximation was used to calculate the most appropriate denominator degrees of freedom for F-tests. Furthermore, least squares means were used in all analyses to adjust for unbalanced sample sizes and initial covariates when appropriate.

Single degree of freedom linear contrasts were constructed to test *a priori* hypotheses about the main and interaction effects of fuel, year and elevation (Table 3.1). Orthogonal linear contrasts for fuel tested three hypotheses. First, I hypothesized that subplots where fuels were unaltered (controls) differed from subplots where fuels were altered, (removal + pine needle addition + wood addition). Second, where fuels were altered, I hypothesized that fuel removal differed from fuel addition, (pine needle addition + wood addition). Finally, addition of pine needles was expected to differ from addition of wood. When a dependent variable was measured in each year (1999, 2000, 2001 and 2002), there were three hypotheses about the effect of year. First, I hypothesized that subplots in the two years following the first fire (1999-2000) differed from the two years following the second fire (2001-2002). Next, two separate contrasts were used to test the hypothesis that there were differences between the first year post-fire and the second year post-fire after each fire. Elevation by fuel contrasts tested the hypothesis that differences among fuel treatment subplots were not the same across elevation plots. Similarly, elevation by year contrasts tested the hypothesis that differences

Table 3.1 Hypotheses associated with linear contrasts for simple and interaction fixed effects used in analyses.

Source of Variation	DF	Questions Addressed
Elevation	1	Do high and low elevation plots differ from each other?
Fuel	3	Do fuel load subplots differ from each other?
Control x (Removal + Needle Addition + Wood Addition)	1	Do unaltered control subplots differ from treated subplots?
Removal x (Needle Addition + Wood Addition)	1	Do subplots with fuels removed differ from subplots with added fuels?
Needle Addition x Wood Addition	1	Do subplots with pine needles added differ from subplots with wood added?
Elevation x Fuel	3	Do fuel load subplots differ in high and low elevation plots?
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	Do unaltered control subplots differ from treated subplots in high and low elevation plots?
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	Do subplots with fuels removed differ from subplots with added fuels in high and low elevation plots?
(Low x High) x (Needle Addition x Wood Addition)	1	Do subplots with pine needles added differ from subplots with wood added in high and low elevation plots?
Year	3	Do subplots change over time?
(1999+2000) x (2001+2002)	1	Do subplots in the two years following the first fire differ from subplots in the two years following the second fire?
1999 x 2000	1	Do subplots differ in the two years following the first fire?
2001 x 2002	1	Do subplots differ in the two years following the second fire?
Elevation x Year	3	Do subplots differ among years in high and low elevation plots?
(Low x High) x [(1999+2000) x (2001+2002)]	1	Do high and low elevation plots differ in the two years following the first fire and the two years following the second fire?
(Low x High) x (1999 x 2000)	1	Do high and low elevation plots differ in the two years following the first fire?
(Low x High) x (2001 x 2002)	1	Do high and low elevation plots differ in the two years following the second fire?

Table 3.1 continued

Fuel x Year	9	Do fuel load subplots differ from each other over time?
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999+2000) x (2001+2002)]	1	Do unaltered control subplots differ from treated subplots in the two years following the first fire and the two years following the second fire?
[(Removal x (Needle Addition + Wood Addition) x [(1999+2000) x (2001+2002)]	1	Do subplots with fuels removed differ from subplots with fuels added in the two years following the first fire and the two years following the second fire?
(Needle Addition x Wood Addition) x [(1999+2000) x (2001+2002)]	1	Do subplots with pine needles added differ from subplots with wood added in the two years following the first fire and the two years following the second fire?
[Control x (Removal + Needle Addition + Wood Addition)] x (1999 x 2000)	1	Do unaltered control subplots differ from treated subplots in the two years following the first fire?
[(Removal x (Needle Addition + Wood Addition)] x (1999 x 2000)	1	Do subplots with fuels removed differ from subplots with fuels added in the two years following the first fire?
(Needle Addition x Wood Addition) x (1999 x 2000)	1	Do subplots with pine needles added differ from subplots with wood added in the two years following the first fire?
[Control x (Removal + Needle Addition + Wood Addition)] x (2001 x 2002)	1	Do unaltered control subplots differ from treated subplots in the two years following the second fire?
[(Removal x (Needle Addition + Wood Addition)] x (2001 x 2002)]	1	Do subplots with fuels removed differ from subplots with fuels added in the two years following the second fire?
(Needle Addition x Wood Addition) x (2001 x 2002)	1	Do subplots with pine needles added differ from subplots with wood added in the two years following the second fire?
Elevation x Fuel x Year	9	Do fuel load subplots differ from each other over time and between high and low elevation plots?

among years were not the same across elevation. Finally, fuel by year contrasts tested that the differences among fuel treatments differed among years. When the model indicated significant main or interaction effects, other specific treatment combinations outside the experimental design of the analysis, were examined as *post hoc* analyses with conservative Tukey-Kramer pair-wise comparisons of least squares means.

Pre-treatment shrub community: Prior to the application of fuel load treatments, shrub community composition and abundance were compared between high and low elevation plots. Analysis of variance in PROC MIXED (SAS Institute 1997) was used to determine the effect of elevation on overall number of stems and number of species. Differences in species abundances are illustrated with dominance-diversity curves (Whittaker 1965).

Resprout density of all species pooled: Treatment effects on natural log transformed (n+1) overall number of resprouts were analyzed using repeated measures analysis of covariance (ANCOVA) in PROC MIXED (SAS Institute 1997). Initial stem density from the pre-treatment census (1998) was used as a covariate. Subplots containing stems that were not top-killed by the preceding fire (<1% in 1999; 2% in 2001) were removed from this analysis. Since the experimental design entailed repeated measurements on the same experimental units, PROC MIXED was used to model both the means and variance-covariance structure of the data. Akaike's Information Criterion and Schwarz's Bayesian Criterion consistently indicated that a compound symmetry variance-covariance structure provided the best-fit model.

Resprout height of all species pooled: Repeated measures analysis of variance (ANOVA) was conducted in PROC MIXED to test for treatment effects on average height of resprouts at the end of the two year period following each fire (2000 and 2002). Resprout

height represented ramet regrowth from complete topkill during the previous year's fire. Ramets that were not topkilled (<1% in each fire) and seedlings (n=16 in 1999; n=22 in 2001) were removed from this analysis.

Species loss or genet mortality: All stems of one species within a subplot were considered to be one genet. Thus species loss from subplots is equivalent to genet mortality. Treatment effects on the probability of species loss from subplots were analyzed with a generalized linear mixed model. Mixed models were generated by invoking PROC MIXED within the GLIMMIX macro (Littell et al. 1996). Models were specified to contain a logit link and a binomial error distribution. The frequency of species loss was determined in each subplot during the two years following each fire. Species were considered lost from a subplot if stems of that species had been present within the subplot prior to fire, but were then absent for two consecutive years following fire. During each post-fire period (1999-2000 and 2001-2002) the condition of species within subplots was recorded as a binomially distributed random variable with species loss (=1) or survival (=0) as the two possible outcomes. Subplots in which no stems of any species were present immediately before the second set of fires (n=28) were excluded from this analysis.

Resprout density of species groups: Resprouting was hypothesized to differ among groups of species that differed in the morphology of underground resprouting organs. Species were divided into three groups: indigenous root crown resprouters (hereafter "root crown"), indigenous rhizome or root sprouters (hereafter "rhizome"), and non-indigenous species (hereafter "exotic"). Treatment effects on natural log (n+1) transformed numbers of stems were analyzed separately for each of the three groups using ANCOVA in PROC MIXED.

The mixed model used for these analyses was the same as that used for density of all species pooled.

Root crown species produced new sprouts almost entirely from the point at the stem base where the meets the root system. Species in this group often produced large numbers of resprouts basal to dead or live stems, but only very infrequently produced sprouts at any distance from the parent plant. Species that were capable of producing resprouts some distance from the parent plant, either along roots or rhizomes, were classified as rhizome resprouters. Some of the rhizome species in this study may not possess true rhizomes, but rather resprout from nodes along lateral roots (del Tredici 2001). However, this results in the same functional outcome, production of potentially autonomous stems some distance from the parent plant. Non-native species varied in their capacity to resprout from root crowns or rhizomes. The most common non-native species and the most common species at the site, *Ligustrum sinense*, resprouts both from root crowns as well as spreads laterally by producing copious root sprouts.

Results

Shrub species composition was similar, but abundances differed, between low and high elevation plots at the onset of the study. A total of 6348 stems of 32 species were counted in the initial census in 1998. Twenty-seven species occurred in the low elevation plots, while 28 occurred in high elevation plots. Neither number of species nor overall stem density differed significantly between high and low elevation plots ($p>0.20$). The same seven species (*Gaylusaccia dumosa, Ilex glabra, I. vomitoria, Ligustrum sinense, Rhus copallinum, Vaccinium arboreum, V. elliotii*) were most abundant in both high and low elevation plots, but the relative abundances of these species differed with elevation (Table 3.2). In low elevation

Table 3.2 Density (stems/m^2) of all hardwood shrub species in low and high elevation plots at CWP at the beginning of the study in 1998. SE=standard error. RC=native root crown species. RH=native rhizomatous species. E=non-native (exotic) species. LI=lignotuber (not included in analyses).

	Low Elevation		High Elevation		Species
Species	**Density**	**SE**	**Density**	**SE**	**Group**
Acer rubrum	0.007	0.007	0.067	0.029	RC
Albizia julibrissin	0	0	0.004	0.004	RC
Aralia spinosa	0.007	0.005	0	0	RH
Callicarpa americana	0.164	0.054	0.146	0.078	RH
Carya tomentosa	0.078	0.028	0.086	0.023	RC
Castanea pumila	0	0	0.011	0.011	RH
Cornus florida	0	0	0.026	0.023	RC
Diospyros virginiana	0.09	0.03	0.075	0.031	RH
Gaylussacia dumosa	0.545	0.182	1.85	0.409	RH
Ilex glabra	0.869	0.354	1.936	0.673	RH
Ilex opaca	0.022	0.022	0	0	RC
Ilex vomitoria	0.776	0.205	0.629	0.196	RC
Ligustrum sinense	5.914	0.687	1.528	0.337	E
Liquidambar styraciflua	0.254	0.068	0.3	0.103	RC
Magnolia virginiana	0	0	0.041	0.041	LI
Malus angustifolia	0.015	0.015	0	0	RC
Morella cerifera	0.194	0.038	0.517	0.124	RH
Nyssa sylvatica	0.138	0.06	0.06	0.038	RC
Prunus serotina	0.179	0.044	0.236	0.063	RC
Quercus falcata	0.06	0.033	0.139	0.078	RC
Quercus marilandica	0.06	0.028	0.105	0.057	RC
Quercus nigra	0.231	0.052	0.176	0.056	RC
Quercus stellata	0.295	0.123	0.139	0.069	RC
Quercus virginiana	0.019	0.01	0.007	0.005	RH
Rhus copallinum	0.772	0.097	1.199	0.118	RH
Sassafras albidum	0.205	0.053	0.262	0.065	RH
Triadica sebifera	0.037	0.027	0.019	0.013	E
Vaccinium arboreum	0.795	0.18	0.67	0.14	RH
Vaccinium darrowii	0	0	0.243	0.162	RH
Vaccinium elliotii	0.653	0.228	0.85	0.247	RH
Vaccinium stamineum	0.015	0.011	0.026	0.014	RH
Viburnum dentatum	0.022	0.022	0	0	RH

plots, absolute density of *Ligustrum sinense* was nearly 6 stems/m^2; densities of other species averaged < 1 stem/m^2. In high elevation plots, no species had a density > 2 stems/m^2, and four species (*Gaylussacia dumosa, I. glabra, Ligustrum sinense, Rhus copallinum)* occurred at densities of > 1 stem/m^2. The densities of shrubs were consistently slightly higher in plots at high compared to low elevations. These differences resulted in different dominance-diversity curves between the two elevations (Figure 3.1).

Effects of Treatments on Probability of Species Loss

Almost all stems were top-killed during fires (>99% in each fire). Both fires resulted in the loss of species from at least some subplots. A total of 1052 (1998) and 1143 (2000) genets were recorded in all plots prior to fires. Of these, 170 and 137 respectively, disappeared from subplots for the two census periods following fire, resulting in an average species loss or genet mortality of ~ 14%.

Elevation, year and interactions: Species loss occurred most frequently at low elevations and following the first fire (Figure 3.2). Average species loss across both years was 16% and 11% in low and high elevation plots, respectively; this difference was significant (p=0.039; Table 3.3). Differences in species loss between years were also significant (p=0.02), with 15% and 12% species loss following the first and second fire, respectively. The decrease in probability of species loss, most noticeable in low elevation plots, resulted in an elevation by year interaction that neared significance (p=0.06).

Fuels: Loss of species increased with the addition of fuels (Figure 3.3). Mortality in wood addition subplots was 22%, more than double that of either unaltered fuels (Tukey-Kramer p=0.001) or fine fuel removals (p=0.0002). Furthermore, mortality in wood addition subplots was 40% greater than that of pine needle addition subplots (contrast p=0.007). Pine

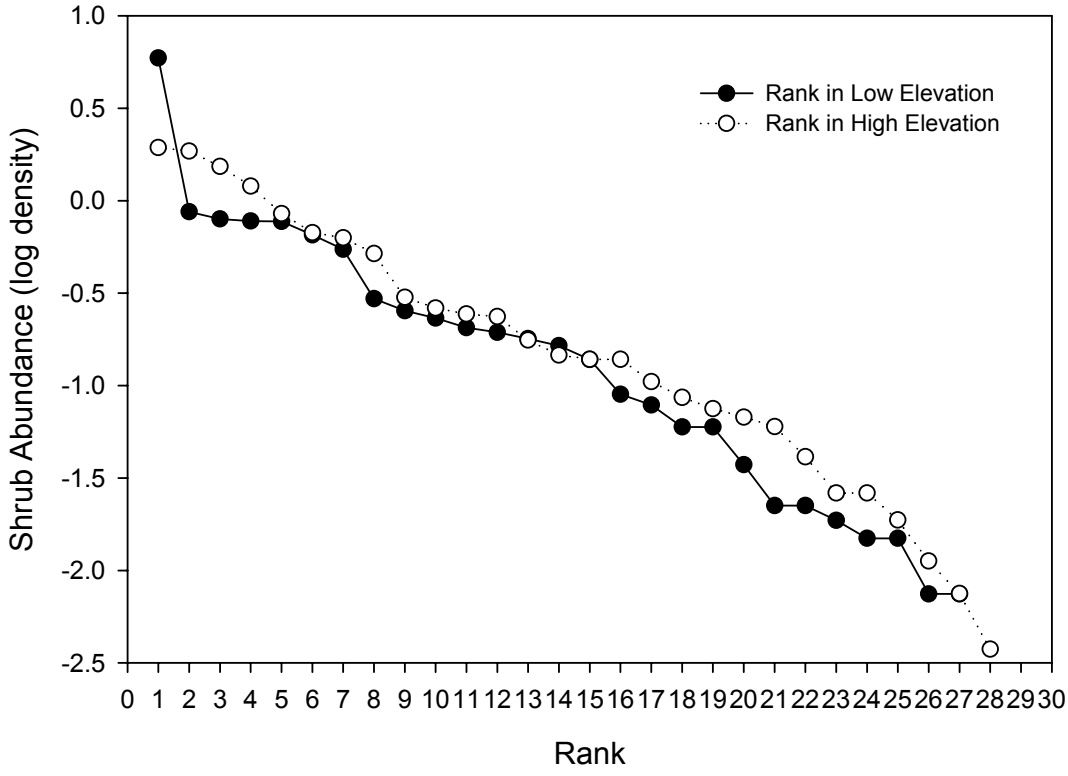


Figure 3.1 Dominance-diversity curves for plots at low and high elevations. For each species, rank abundance in each plot type is plotted against log density for that species in that plot type.

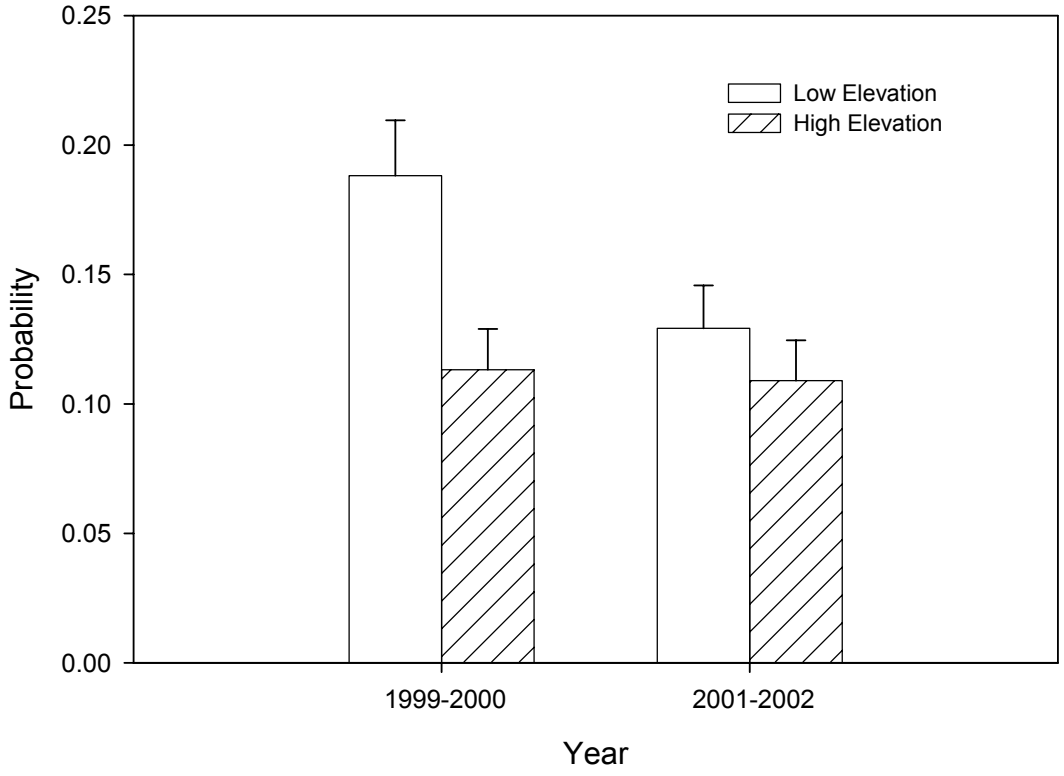


Figure 3.2 Estimated probability of species loss (genet mortality) from subplots within high and low elevation plots after fire 1 (1999-2000) and fire 2 (2001-2002). Bars represent least squares means $\pm$ SE of probabilities back-transformed from logits.

Table 3.3 Results of generalized linear mixed model analysis of the probability of species loss (genet mortality). Species loss is defined as presence of stems of a species prior to fire, but absence of all stems of that species for two consecutive years post-fire. Error term for Elevation = Elevation x Transect(Ravine); Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)); Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	10.1	5.63	0.0388	*
Fuel	3	433	6.54	0.0002	*
Elevation x Fuel	3	433	0.48	0.698	
Year	1	592	5.32	0.0214	*
Elevation x Year	1	592	3.61	0.0579	
Fuel x Year	3	591	2.95	0.0323	*
Elevation x Fuel x Year	3	591	1.23	0.2988	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	447	4.48	0.0349	*
Removal x (Needle Addition + Wood Addition)	1	451	14.12	0.0002	*
Needle Addition x Wood Addition	1	374	7.3	0.0072	*
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	446	0	0.999	
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	452	0.36	0.548	
(Low x High) x (Needle Addition x Wood Addition)	1	374	0.73	0.394	
Fuel x Year:					
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999-2000) x (2001-2002)]	1	588	6.28	0.013	*
[(Removal x (Needle Addition + Wood Addition) x [(1999-2000) x (2001-2002)]	1	593	2.94	0.087	
(Needle Addition x Wood Addition) x [(1999-2000) x (2001-2002)]	1	595	0.03	0.854	

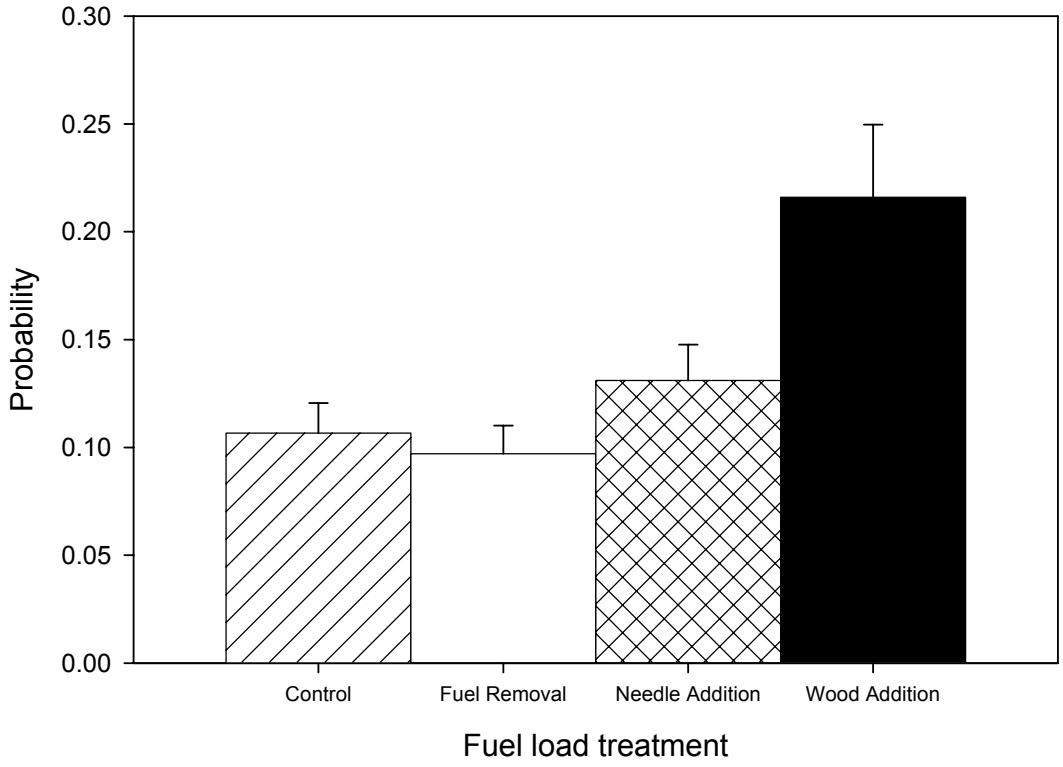


Figure 3.3 Estimated probability of species loss (genet mortality) from subplots receiving one of four fuel load treatments. Bars represent least squares means $\pm$ SE of probabilities back-transformed from logits.

needle addition did not significantly increase species loss relative to either unaltered fuels or fuel removals (Tukey-Kramer p-values>0.23). Fuels affected genet mortality to a larger extent following the first fire (Figure 3.4), as indicated by a significant fuel by year interaction (p=0.03). The difference between species loss in unaltered controls and treated subplots was greater following the first than second fire (p=0.013).

Effects of Treatments on Resprouting Dynamics: Resprout Density and Height of All Species Pooled

At least some stems of all species resprouted following fires. Resprouting of some shrub species began as early as 2 weeks post-fire, and all species had begun to resprout 2 months post-fire. Initial differences in stem density within subplots were most important in determining post-fire abundance of resprouting stems; the F-value for the covariate (F=651.45, p<0.0001) was more than an order of magnitude larger than that for any other effect in the model.

Year, elevation and interactions: Stem densities increased over time, but stem heights decreased. After adjusting for the covariate, resprout density increased from 7.7 stems/m^2 in 1999 to 9.5 stems/m^2 in 2002 (Figure 3.5). Furthermore, resprout density was higher during the two-year period following the second fire (2001-2002) than following the first fire (1999-2000; linear contrast p<0.0001, Table 3.4). During the two-year period after each fire, densities of resprouting stems increased from 2 months after fire to 14 months post-fire (p<0.0001 for 1999-2000, p=0.0294 for 2001-2002). Conversely, heights decreased over time (Figure 3.6). Average height of stems was nearly 2 centimeters less 14 months after the second compared to the first fire (p=0.001, Table 3.5).

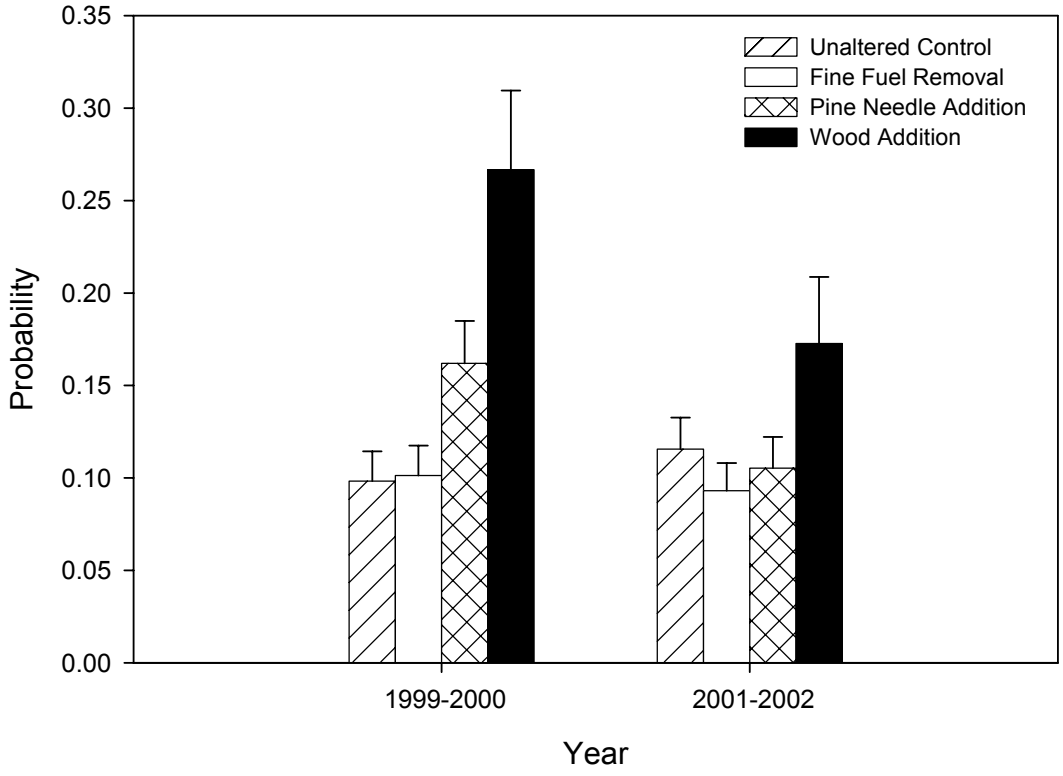


Figure 3.4 Estimated probability of species loss (genet mortality) from fuel load treatment subplots during the two year period following fires in 1999 and 2001. Bars represent least squares means $\pm$ SE of probabilities back-transformed from logits.

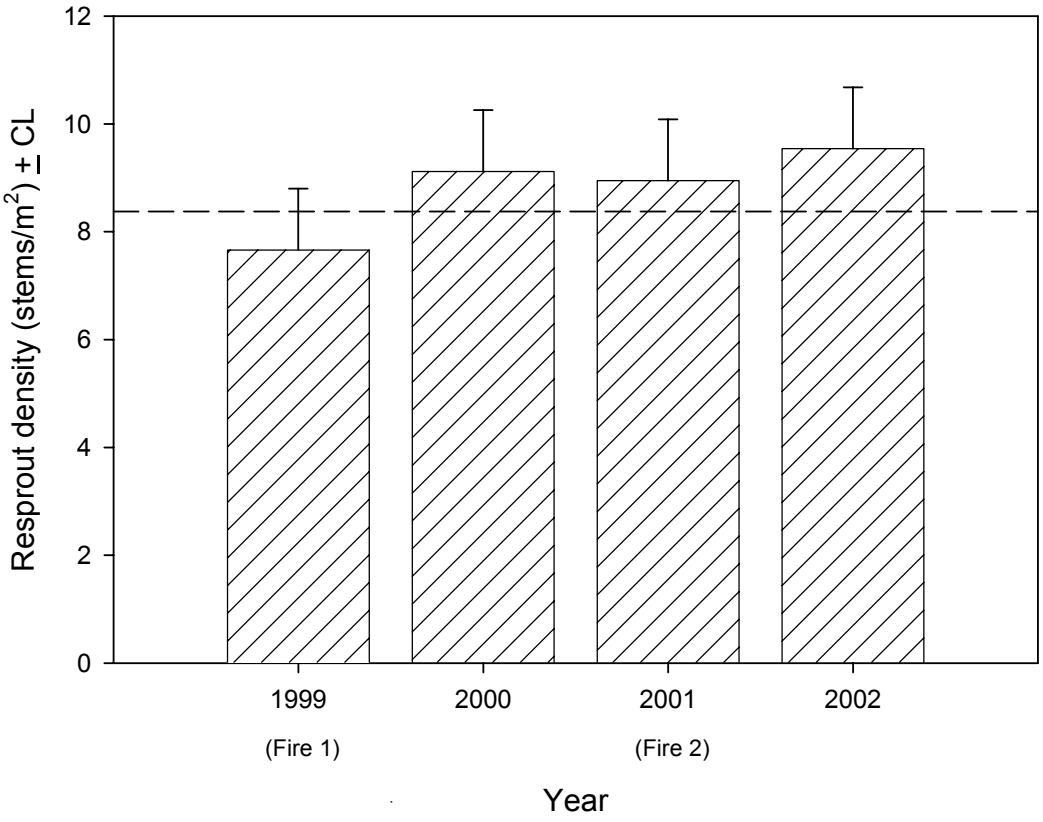


Figure 3.5 Overall resprout density (stems/m^2) of all species pooled at 2 months and 14 months following each fire. Mean values for each year are back-transformed least square means adjusted for differences in initial pre-treatment (1998) density. The dashed line is placed at the mean value of the initial covariate. Error bars are 95% confidence intervals for estimated means.

Table 3.4 Results of mixed model repeated measures ANCOVA of stem density for all species pooled. Covariate = 1998 initial stem density. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Covariance structure = compound symmetry.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Covariate	1	473	651.45	<0.0001	*
Elevation	1	12.5	4.31	0.0591	
Fuel	3	496	20.01	<0.0001	*
Elevation x Fuel	3	496	0.98	0.402	
Year	3	1537	20.88	<0.0001	*
Elevation x Year	3	1537	2.94	0.0322	*
Fuel x Year	9	1537	2.67	0.0044	*
Elevation x Fuel x Year	9	1537	0.54	0.8436	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	496	27.39	<0.0001	*
Removal x (Needle Addition + Wood Addition)	1	497	40.36	<0.0001	*
Needle Addition x Wood Addition	1	496	13.41	0.0003	*
Linear Contrasts (Year):					
(1999+2000) x (2001+2002)	1	1537	22.98	<0.0001	*
1999 x 2000	1	1537	34.67	<0.0001	*
2001 x 2002	1	1537	4.75	0.0294	*
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	496	0.06	0.8132	
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	497	0.05	0.829	
(Low x High) x (Needle Addition x Wood Addition)	1	496	2.49	0.115	
Elevation x Year:					
(Low x High) x [(1999+2000) x (2001+2002)]	1	1537	2.91	0.088	
(Low x High) x (1999 x 2000)	1	1537	5.23	0.022	*
(Low x High) x (2001 x 2002)	1	1537	0.64	0.425	

Table 3.4 continued

Fuel x Year:					
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999+2000) x (2001+2002)]	1	1537	0.05	0.829	
[(Removal x (Needle Addition + Wood Addition) x [(1999+2000) x (2001+2002)]	1	1538	0.54	0.462	
(Needle Addition x Wood Addition) x [(1999+2000) x (2001+2002)]	1	1537	9.55	0.002	*
[Control x (Removal + Needle Addition + Wood Addition)] x (1999 x 2000)	1	1536	1.04	0.3074	
[(Removal x (Needle Addition + Wood Addition)] x (1999 x 2000)	1	1537	9.3	0.002	*
(Needle Addition x Wood Addition) x (1999 x 2000)	1	1537	1.38	0.241	
[Control x (Removal + Needle Addition + Wood Addition)] x (2001+2002)	1	1537	0.03	0.863	
[(Removal x (Needle Addition + Wood Addition)] x (2001+2002)]	1	1536	3.38	0.066	
(Needle Addition x Wood Addition) x (2001+2002)	1	1536	0.19	0.666	

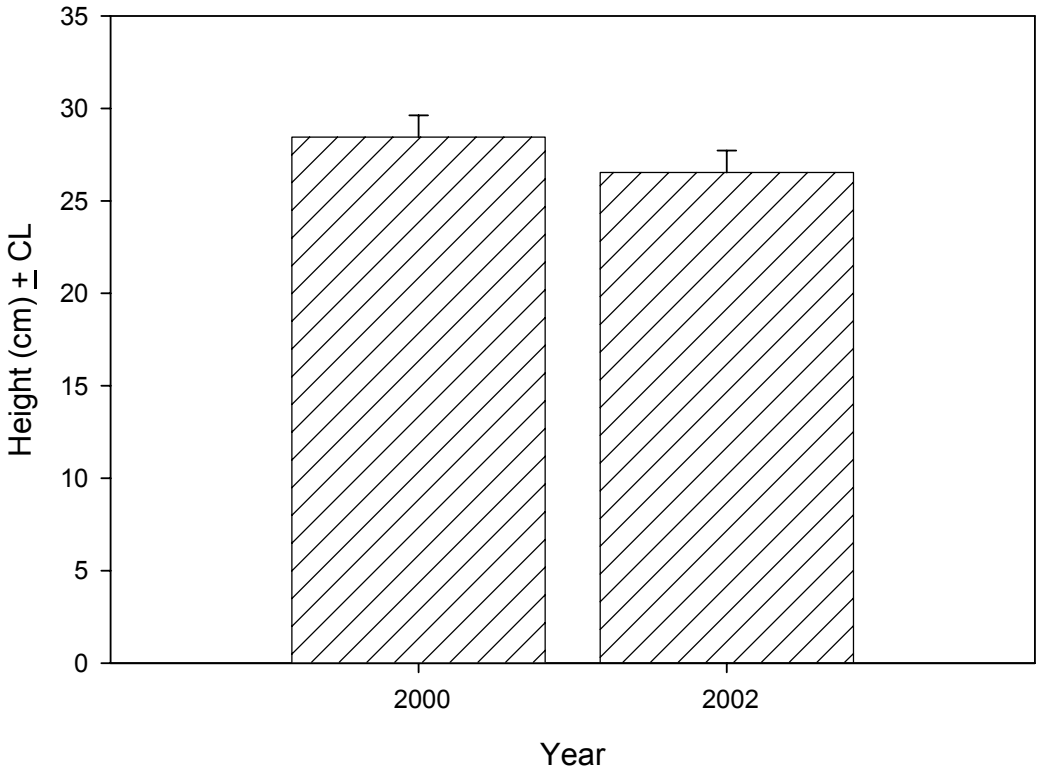


Figure 3.6 Mean height (cm) of resprouts of all species pooled at 14 months following each fire. Mean height is presented as back-transformed least squares means ± 95% confidence intervals.

Table 3.5 Results of mixed model repeated measures ANOVA of stem height for all species pooled. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Elevation	1	10.2	1.17	0.3045	
Fuel	3	497	2.2	0.0874	
Elevation x Fuel	3	497	2.94	0.0327	*
Year	1	494	10.97	0.001	*
Elevation x Year	1	494	0.8	0.3712	
Fuel x Year	3	488	2.51	0.0577	
Elevation x Fuel x Year	3	488	0.73	0.5325	
Linear Contrasts:					
Control x (Removal + Needle Addition + Wood Addition)	1	493	3.2	0.0744	
Removal x (Needle Addition + Wood Addition)	1	500	4.05	0.0446	*
Needle Addition x Wood Addition	1	506	0.11	0.7447	
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	493	2.22	0.137	
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	500	4.86	0.0279	*
(Low x High) x (Needle Addition x Wood Addition)	1	506	5.85	0.016	*
Fuel x Year:					
[Control x (Removal + Needle Addition + Wood Addition)] x [(2000) x (2002)]	1	484	1.87	0.172	
[(Removal x (Needle Addition + Wood Addition) x [(2000) x (2002)]	1	492	2.2	0.139	
(Needle Addition x Wood Addition) x [(2000) x (2002)]	1	501	1.2	0.274	

Elevation had only marginal effects on resprout density and no effect on height. High and low elevation plots averaged 9 and 8 stems/m^2 , respectively; this difference was marginally significant (p=0.059). Average stem heights in high and low elevation plots were not significantly different (p=0.30, Table 3.5). Although low elevation plots contained fewer stems than high plots in each year of the study (Figure 3.7), a significant elevation by year interaction for resprout density (p=0.032) resulted from differences in stem densities between elevations that were significantly greater in 1999 than 2000 (p=0.022).

Fuels and interactions: Resprout number was decreased by the addition of fuels, but unaffected by fuel removal. After adjusting for initial pre-treatment differences in stem number, pine needle addition subplots contained 25% fewer, and wood addition subplots 50% fewer, resprouts than either unaltered controls or fine fuel removals (Figure 3.8a). Overall treatment differences were significant (p<0.0001, Table 3.4). Linear contrasts indicated that differences between fuel removal treatments and fuel addition treatments were highly significant (p<0.0001), as were differences between needle addition treatments and wood addition treatments (p=0.0003). Furthermore, unaltered controls differed significantly between pine needle addition (Tukey-Kramer p=0.0002) and wood addition subplots (Tukey-Kramer p<0.0001), but unaltered controls did not differ significantly from fine fuel removals.

Fuel treatments did not affect resprout height to the same extent as resprout number. Resprout height tended to be lower in fuel addition subplots than fuel removal subplots (Figure 3.8b). The overall treatment effect of fuel was not significant (p=0.09, Table 3.5), but a planned linear contrast between fuel removals and fuel additions was significant (p=0.045).

Fuel load effects on height were more pronounced at high elevation than low elevation (Figure 3.9), resulting in a significant elevation by fuel interaction (p=0.03, Table 3.5).

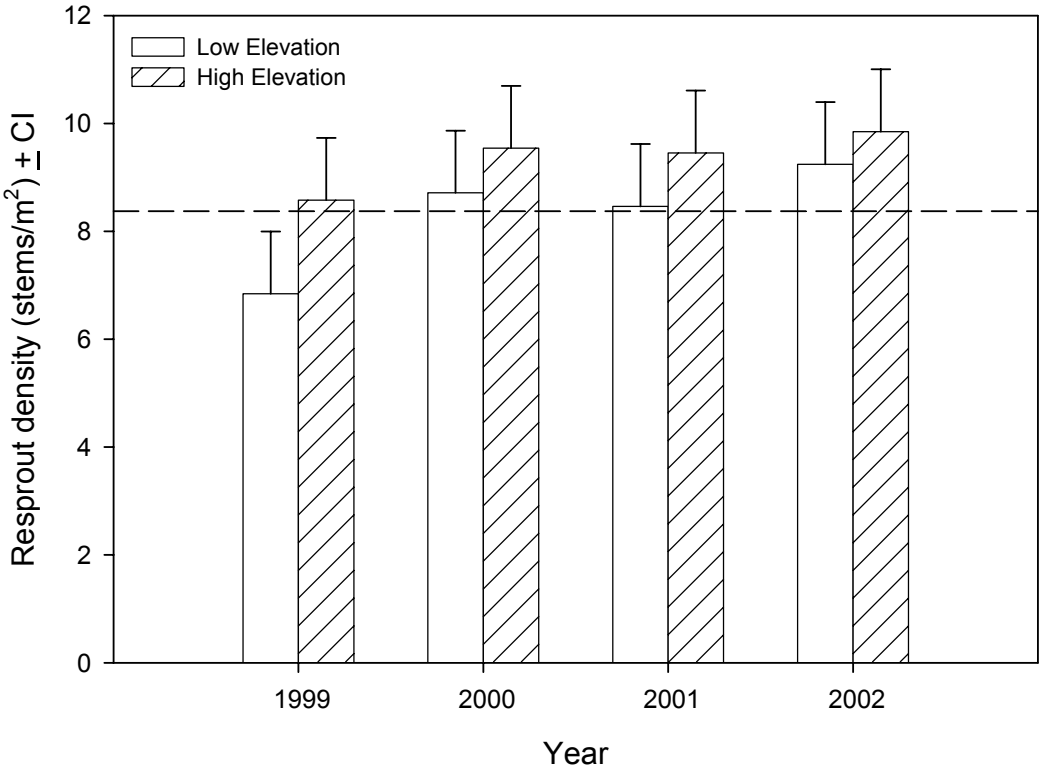


Figure 3.7 Mean resprout density (stems/m^2) of all species pooled within elevation plots by year. Bars represent back-transformed least squares means adjusted for the initial covariate (1998 stem density). Error bars are 95% confidence intervals of estimated means. Dashed line indicates the mean of the initial covariate.

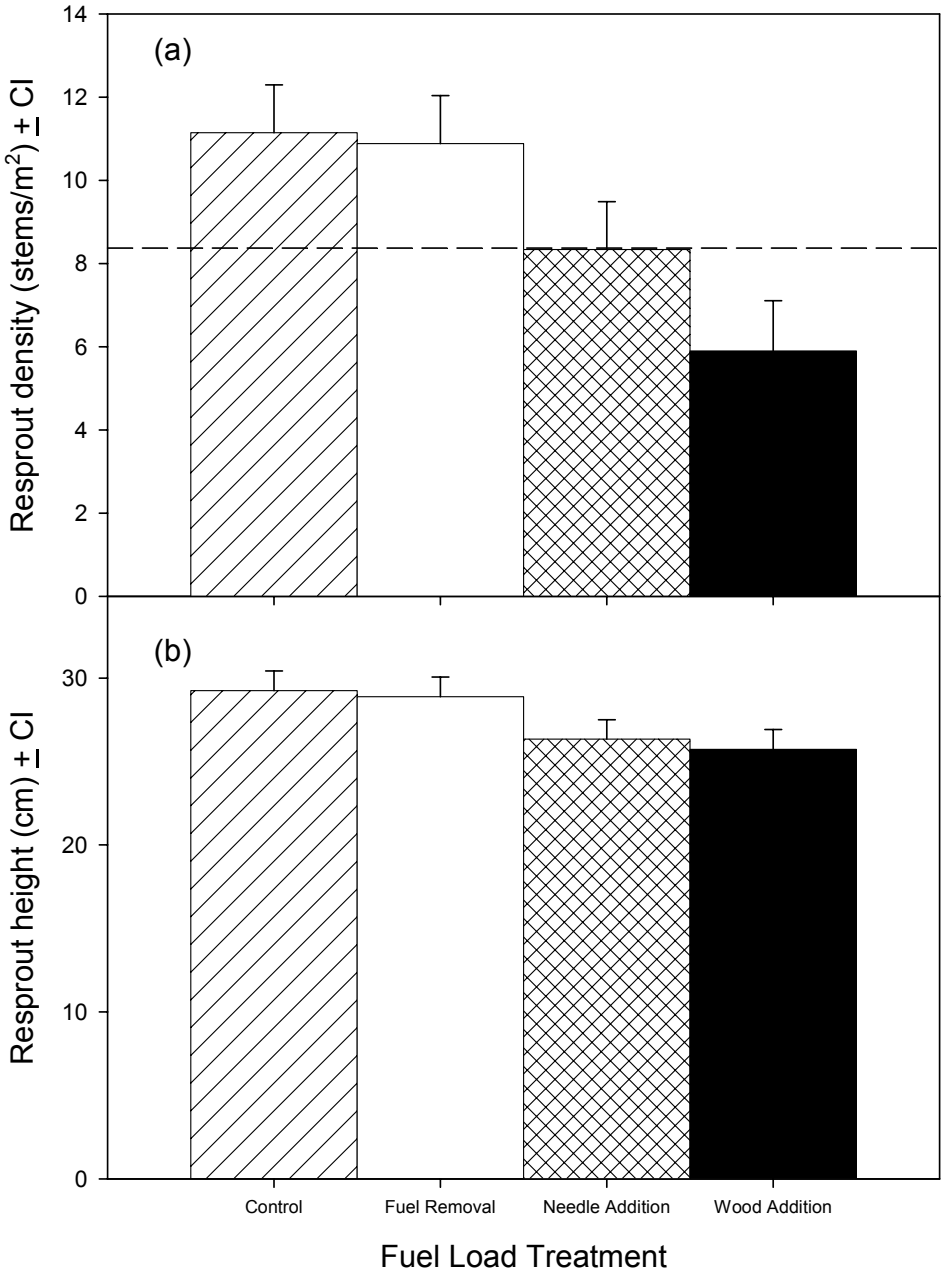


Figure 3.8 (a) Resprout density (stems/m^2) and **(b)** resprout height (cm) of all species pooled at each level of fuel load treatment: unaltered fuel (control), fine fuel removal, pine needle addition and wood addition. All bars are back transformed least squares means (± 95% confidence interval). Least squares are adjusted for initial (1998) stem densities. Horizontal dashed line in (a) indicates the mean of the mean of the initial covariate.

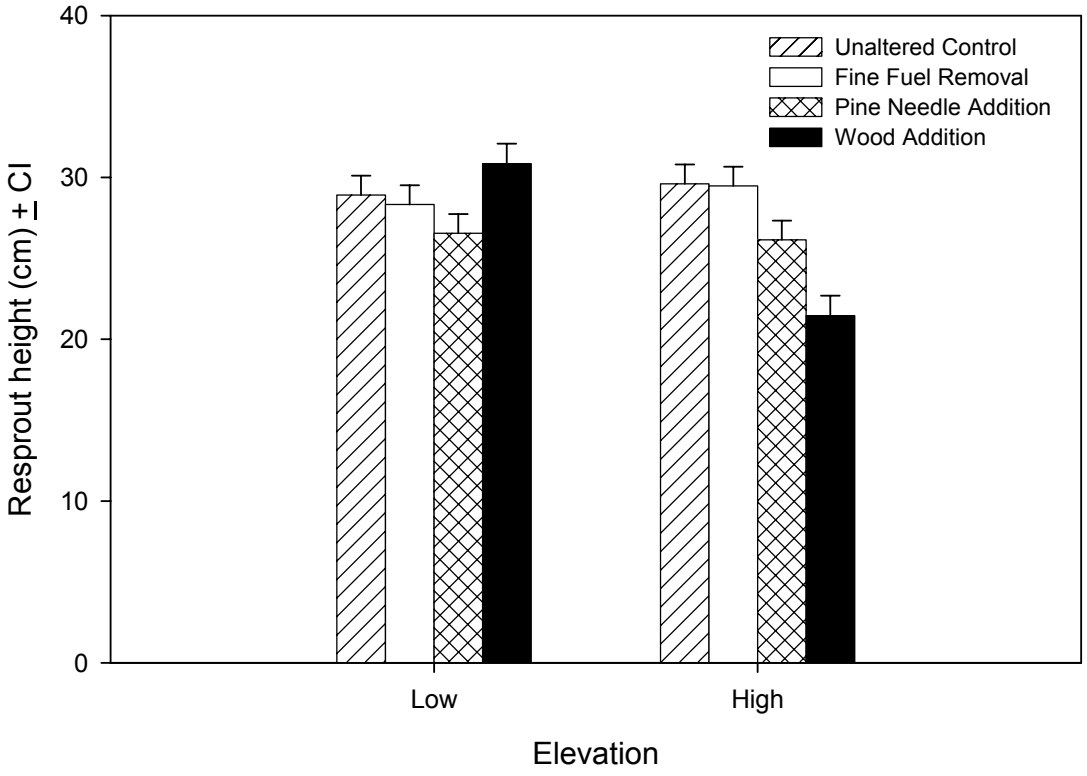


Figure 3.9 Resprout height (cm) of all species pooled in fuel load treatment subplots located at low and high elevations. Bars are back transformed least squares means ± 95% confidence interval.

Differences between fuel removal and fuel addition subplots were greater at high elevation plots ($p=0.03$), as were differences between wood addition and pine needle addition subplots ($p=0.02$). Within high elevation plots, wood addition produced a nearly 8 cm reduction in shrub height relative to either unaltered controls or fine fuel removals (Tukey-Kramer $p=0.03$), while differences among fuel load treatments within low elevation plots were not significant.

Fuel effects on resprouting varied over time resulting in a significant fuel by year interaction ($p=0.004$, Table 3.4). In all years, resprout density in unaltered controls and fine fuel removals tended to be higher than that of pine needle addition subplots and wood addition subplots (Figure 3.10). However differences between fuel removals and added fuels tended to be greatest in the first year following each fire. Linear contrasts for differences between fuel removal and fuel addition subplots were significant between the two years following the first fire ($p=0.002$) and marginally so following the second fire ($p=0.066$). Furthermore, the negative effect of wood addition relative to pine needle addition was greater following the first fire than following the second ($p=0.002$).

Effects of Treatments on Resprouting of Species Groups: Rhizome, Root Crown and Exotic

Elevation, year and interactions: Densities of the three groups changed differently over time. Native rhizomatous species density increased an average of 1 stem/subplot from 1999 to 2001 (Figure 3.11a). Overall effects of year were highly significant for these species ($p<0.0001$, Table 3.6); the density increased from 1999 to 2000 ($p<0.0001$), but did not change from 2001 to 2002. Density of root crown species remained generally unchanged over time (Figure 3.11b). The year main effect was not significant ($p=0.124$), but linear contrasts

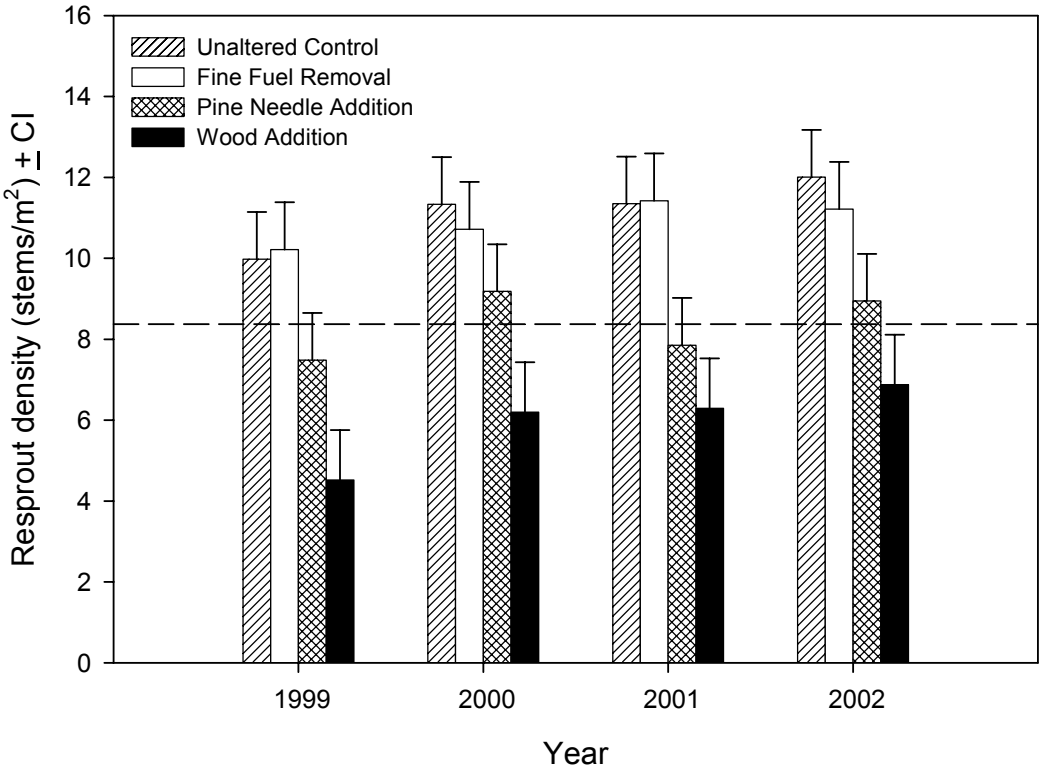


Figure 3.10 Resprout density of all species pooled within fuel load treatments by year. Bars are back transformed least square means adjusted for the covariate (1998 density). Error bars are 95% confidence intervals of estimated means. Dashed line indicates the mean of the covariate.

Figure 3.11 Resprout density by year of **(a)** indigenous rhizome resprouters, **(b)** indigenous root crown resprouters and **(c)** non-indigenous species. Bars are back-transformed least squares means $\pm$ 95% confidence interval adjusted for the initial covariate (1998 density). Dashed line is initial covariate for each species group.

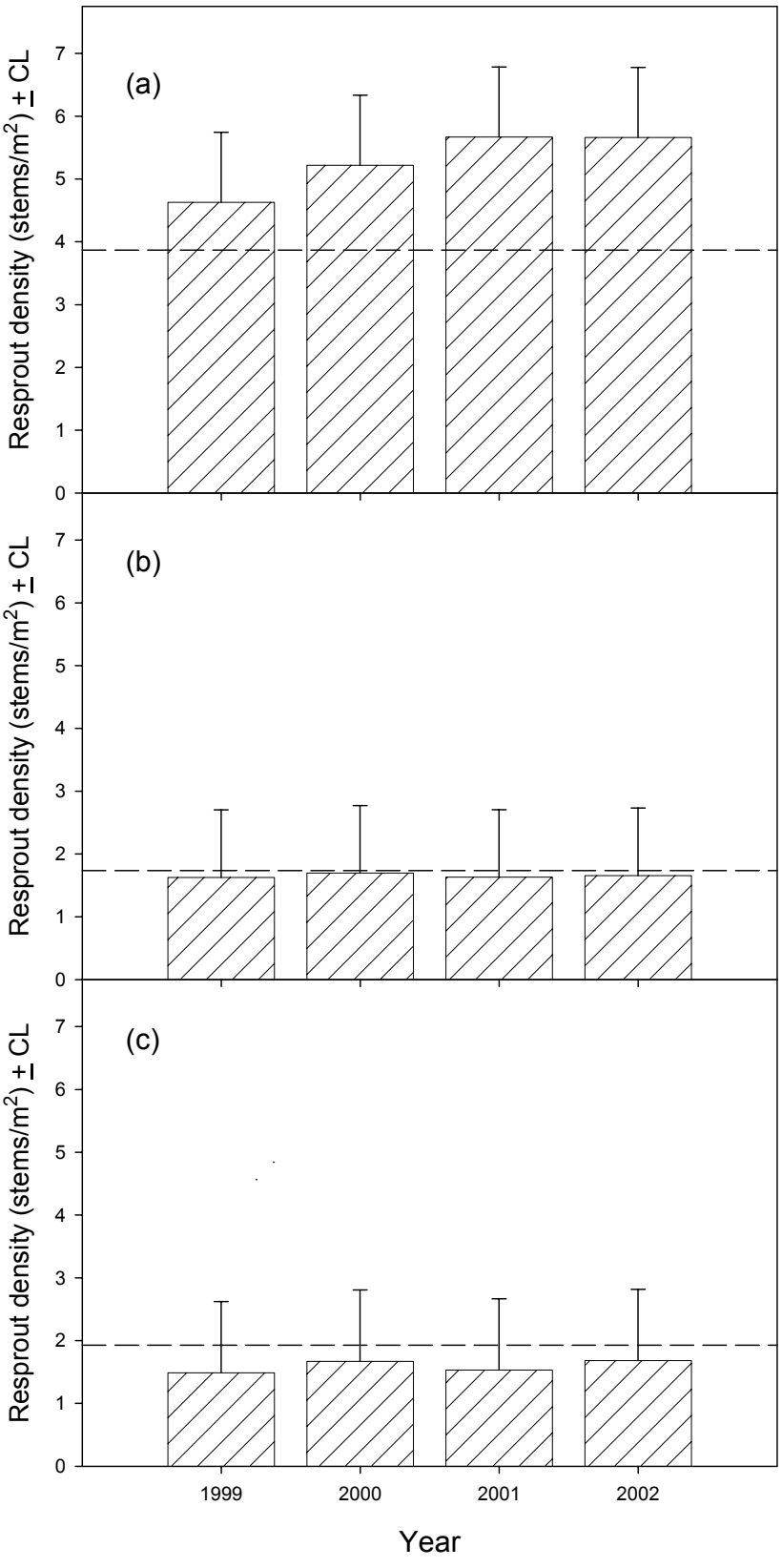

(a)
(b)
(c)
Resprout density (stems/m2) ± CL
0
1
2
3
4
5
6
7
1999
2000
2001
2002
Year

Table 3.6 Results of mixed model repeated measures ANCOVA of stem density for native rhizomatous species. Covariate = 1998 initial stem density. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Covariance structure = compound symmetry.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Covariate	1	506	834.55	<0.0001	*
Elevation	1	11.7	1.2	0.2946	
Fuel	3	506	6.89	0.0001	*
Elevation x Fuel	3	506	4.54	0.0037	*
Year	3	1572	21.58	<0.0001	*
Elevation x Year	3	1572	1.93	0.1222	
Fuel x Year	9	1572	1.87	0.053	
Elevation x Fuel x Year	9	1572	1.09	0.3702	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	505	11.61	0.0007	*
Removal x (Needle Addition + Wood Addition)	1	506	11.96	0.0006	*
Needle Addition x Wood Addition	1	507	5.02	0.0255	*
Linear Contrasts (Year):					
(1999+2000) x (2001+2002)	1	1572	47.74	<0.0001	*
1999 x 2000	1	1572	17	<0.0001	*
2001 x 2002	1	1572	0	0.9656	
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	505	3.92	0.048	*
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	506	5.84	0.016	*
(Low x High) x (Needle Addition x Wood Addition)	1	506	10.2	0.002	*
Elevation x Year:					
(Low x High) x [(1999+2000) x (2001+2002)]	1	1572	4.12	0.043	*
(Low x High) x (1999 x 2000)	1	1572	1.4	0.236	
(Low x High) x (2001 x 2002)	1	1572	0.27	0.601	

Table 3.6 continued

Fuel x Year:					
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999+2000) x (2001+2002)]	1	1572	3.25	0.072	
[(Removal x (Needle Addition + Wood Addition) x [(1999+2000) x (2001+2002)]	1	1572	0.64	0.425	
(Needle Addition x Wood Addition) x [(1999+2000) x (2001+2002)]	1	1572	7.67	0.006	*
[Control x (Removal + Needle Addition + Wood Addition)] x (1999 x 2000)	1	1572	0.01	0.926	
[(Removal x (Needle Addition + Wood Addition)] x (1999 x 2000)	1	1572	0.42	0.517	
(Needle Addition x Wood Addition) x (1999 x 2000)	1	1572	2.82	0.093	
[Control x (Removal + Needle Addition + Wood Addition)] x (2001+2002)	1	1572	2.28	0.131	
[(Removal x (Needle Addition + Wood Addition)] x (2001+2002)]	1	1572	3.1	0.079	
(Needle Addition x Wood Addition) x (2001+2002)	1	1572	0.25	0.617	

indicated a marginally significant increase from 2 months to 14 months after the first fire ($p=0.04$, Table 3.7). Exotic species tended to increase from the first year post-fire to the second year after each fire (Figure 3.11c). These changes resulted in significant differences between the first and second years after each fire (p-values <0.0001 and 0.0003, Table 3.8), but there was no overall increase from the beginning to the end of the study ($p=.3328$).

Elevation affected resprouting of exotic species but not native species. Initial density of exotic species was more than 3 times larger at low elevations than at high elevations. During the study, density was proportionally more reduced at low elevations than at high elevations resulting in a significant elevation effect ($p=0.0324$, Table 3.8). Density at low elevations increased differently from that at high elevations, resulting in a significant elevation by year interaction ($p=0.011$). Specifically, the largest effects of fire on exotics occurred in low elevation plots in 1999, the first year after the first fire ($p=0.016$).

Fuel and interactions: After adjusting for significant differences in initial density ($p<0.0001$) for all species groups, fuel addition decreased resprouting of all three groups of species, but the effects were larger for rhizome and exotic species than for root crown species. For both rhizomatous and exotic species, addition of either pine needle or wood fuels reduced resprouting nearly 20% relative to fuel removals and 25% relative to unaltered controls (Figure 3.12a,c). Also, addition of wood reduced resprouting for both groups nearly 20% below that of pine needle addition plots. The overall effect of fuel additions was significant for both rhizome ($p=0.001$) and exotic species ($p<0.0001$), as were all linear contrasts among fuel treatments (Tables 3.6, 3.8). For neither group did resprouting differ among unaltered controls and fine fuel removals. Resprouting of root crown species also differed among fuel treatments ($p=0.0124$, Table 3.7), but these effects were primarily a result of the 17 %

Table 3.7 Results of mixed model repeated measures ANCOVA of stem density for native root crown species. Covariate = 1998 initial stem density. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Covariance structure = compound symmetry.

Source of Variation	NDF	DDF	F	p	
Fixed Effects:					
Covariate	1	525	1309.61	<0.0001	*
Elevation	1	10.2	0.81	0.3928	
Fuel	3	517	3.66	0.0124	*
Elevation x Fuel	3	517	0.09	0.9644	
Year	3	1579	1.92	0.124	
Elevation x Year	3	1579	0.28	0.8416	
Fuel x Year	9	1579	0.72	0.6868	
Elevation x Fuel x Year	9	1579	0.61	0.7907	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	517	2.44	0.1189	
Removal x (Needle Addition + Wood Addition)	1	518	9.77	0.0019	*
Needle Addition x Wood Addition	1	517	0.75	0.3867	
Linear Contrasts (Year):					
(1999+2000) x (2001+2002)	1	1579	0.58	0.4446	
1999 x 2000	1	1579	4.52	0.0338	*
2001 x 2002	1	1579	0.67	0.4143	
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	517	0.04	0.842	
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	518	0.18	0.672	
(Low x High) x (Needle Addition x Wood Addition)	1	517	0.05	0.823	
Elevation x Year:					
(Low x High) x [(1999+2000) x (2001+2002)]	1	1579	0.2	0.658	
(Low x High) x (1999 x 2000)	1	1579	0.09	0.763	
(Low x High) x (2001 x 2002)	1	1579	0.55	0.46	

Table 3.7 continued

Fuel x Year:				
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999+2000) x (2001+2002)]	1	1579	1.62	0.204
[(Removal x (Needle Addition + Wood Addition) x [(1999+2000) x (2001+2002)]	1	1580	0.74	0.389
(Needle Addition x Wood Addition) x [(1999+2000) x (2001+2002)]	1	1579	0.81	0.369
[Control x (Removal + Needle Addition + Wood Addition)] x (1999 x 2000)	1	1579	0	0.989
[(Removal x (Needle Addition + Wood Addition)] x (1999 x 2000)	1	1579	0.4	0.525
(Needle Addition x Wood Addition) x (1999 x 2000)	1	1579	0.18	0.669
[Control x (Removal + Needle Addition + Wood Addition)] x (2001+2002)	1	1579	1.07	0.3
[(Removal x (Needle Addition + Wood Addition)] x (2001+2002)]	1	1579	1.16	0.281
(Needle Addition x Wood Addition) x (2001+2002)	1	1579	0.08	0.776

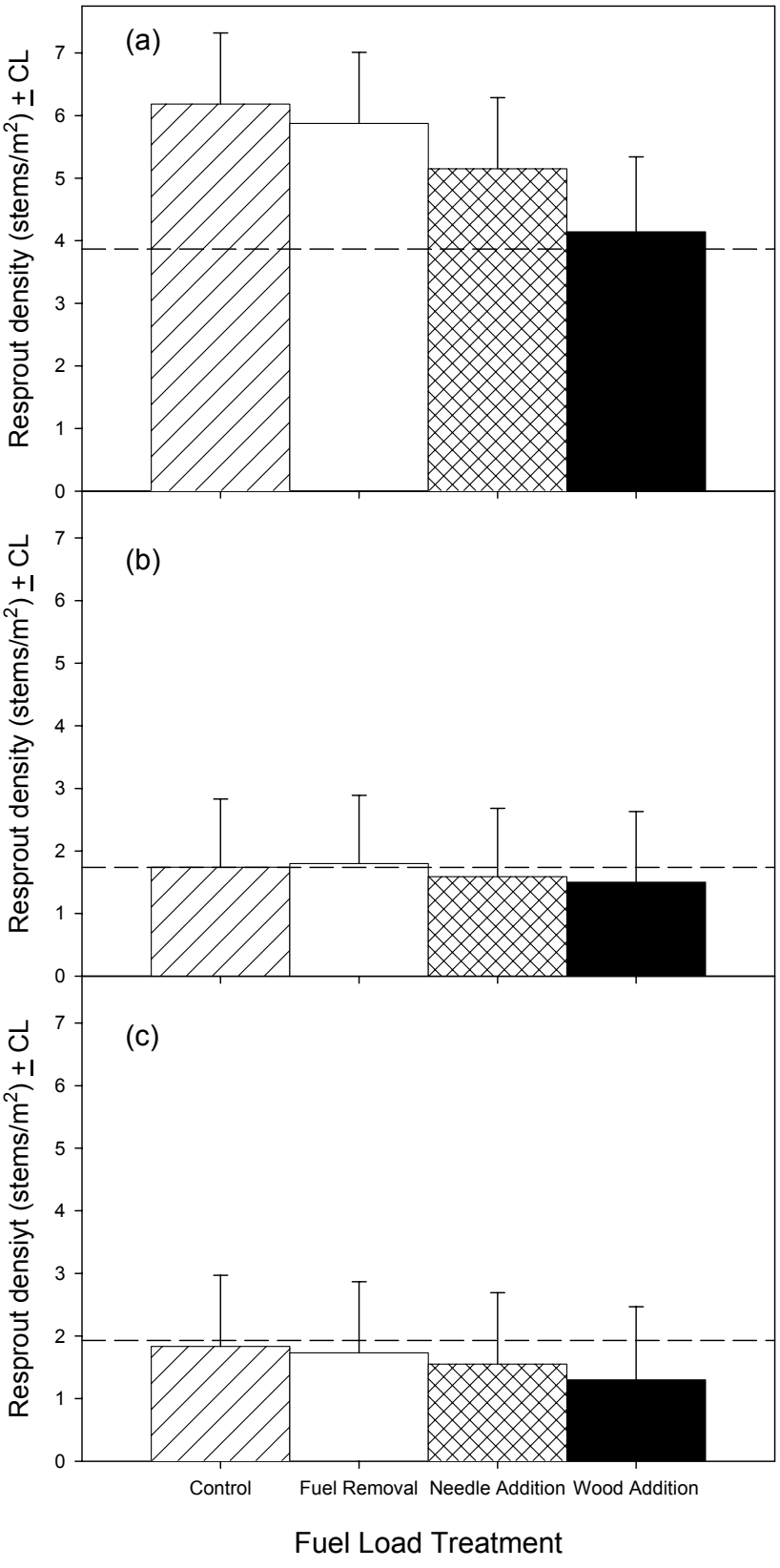
Table 3.8 Results of mixed model repeated measures ANCOVA of stem density for exotic species. Covariate = 1998 initial stem density. Error term for Elevation = Elevation x Transect(Ravine). Error term for Fuel and interactions = Subplot(Fuel x Elevation x Transect(Ravine)). Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Covariance structure = compound symmetry.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Covariate	1	477	12393.52	<0.0001	*
Elevation	1	12.3	5.82	0.0324	*
Fuel	3	508	8.95	<0.0001	*
Elevation x Fuel	3	508	4.82	0.0026	*
Year	3	1581	11.56	<0.0001	*
Elevation x Year	3	1581	2.83	0.0371	*
Fuel x Year	9	1581	2.4	0.0105	*
Elevation x Fuel x Year	9	1581	1.21	0.2857	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	508	16.46	<0.0001	*
Removal x (Needle Addition + Wood Addition)	1	509	14.21	0.0002	*
Needle Addition x Wood Addition	1	508	6.01	0.0145	*
Linear Contrasts (Year):					
(1999+2000) x (2001+2002)	1	1581	0.94	0.3328	
1999 x 2000	1	1581	20.62	<0.0001	*
2001 x 2002	1	1581	13.1	0.0003	*
Elevation x Fuel:					
(Low x High) x [Control x (Removal + Needle Addition + Wood Addition)]	1	508	8.7	0.003	*
(Low x High) x [(Removal x (Needle Addition + Wood Addition)]	1	509	7.99	0.0049	*
(Low x High) x (Needle Addition x Wood Addition)	1	508	2.81	0.094	
Elevation x Year:					
(Low x High) x [(1999+2000) x (2001+2002)]	1	1581	0.16	0.692	
(Low x High) x (1999 x 2000)	1	1581	5.87	0.016	*
(Low x High) x (2001 x 2002)	1	1581	2.47	0.116	

Table 3.8 continued

Fuel x Year:					
[Control x (Removal + Needle Addition + Wood Addition)] x [(1999+2000) x (2001+2002)]	1	1581	1.87	0.172	
[(Removal x (Needle Addition + Wood Addition) x [(1999+2000) x (2001+2002)]	1	1581	3.68	0.055	
(Needle Addition x Wood Addition) x [(1999+2000) x (2001+2002)]	1	1581	3.7	0.055	
[Control x (Removal + Needle Addition + Wood Addition)] x (1999 x 2000)	1	1581	1.52	0.218	
[(Removal x (Needle Addition + Wood Addition)] x (1999 x 2000)	1	1581	5.86	0.016	*
(Needle Addition x Wood Addition) x (1999 x 2000)	1	1581	0.33	0.567	
[Control x (Removal + Needle Addition + Wood Addition)] x (2001+2002)	1	1581	0.15	0.695	
[(Removal x (Needle Addition + Wood Addition)] x (2001+2002)]	1	1581	1.34	0.247	
(Needle Addition x Wood Addition) x (2001+2002)	1	1581	2.06	0.151	

Figure 3.12 Resprout density within fuel load treatments for **(a)** indigenous rhizome resprouters, **(b)** indigenous root crown resprouters and **(c)** non-indigenous species. Bars are back-transformed least squares means $\pm$ 95% confidence interval adjusted for the initial covariate (1998 density). Dashed line is initial covariate for each species group.


(a)
(b)
(c)
Resprout density (stems/m2) ± CL
Resprout density (stems/m2) ± CL
Resprout densiyt (stems/m2) ± CL
0
1
2
3
4
5
6
7
Control
Fuel Removal
Needle Addition
Wood Addition
Fuel Load Treatment

reduction in density in wood addition plots relative to fuel removals (Figure 3.12b). Linear contrasts indicated that differences among plots with fuels added and plots with fuels removed were significant (p=0.0019), however there was no reduction in wood addition subplots relative to pine needle addition (p=0.39), nor differences between unaltered controls and treatments (p=0.119).

Fuel load effects were variable over both time and elevation for rhizome species and exotic species, but not root crown species. Differences among fuel load treatments for both rhizome and exotic species tended to be greater after the first fire and particularly during the first year after fire, resulting in significant fuel by year interactions (rhizome p=0.05; exotic p=0.011). The difference between wood addition and needle addition treatments for rhizomatous species was greater following the first fire than following the second fire (p=0.006, Table 3.6). For exotic species, the difference between fuel removal and fuel addition tended to be greater in the first year following the first fire than in the second year following the first fire (p=0.016, Table 3.8). Differences among fuel load treatments tended to be greater at higher elevations for rhizome species and at low elevations for exotic species. Elevation by fuel interactions were significant for both groups of species (rhizome p=0.004; exotic p=0.003). For rhizome species, the difference between all fuel load contrasts was greater at high elevation than low elevations (Table 3.6). For exotic species, the pattern was reversed with the difference between both unaltered controls and treated subplots (p=0.003, Table 3.8) and the difference between fuel removals and fuel additions (p=0.0049) greater at low elevations than at high elevations.

Discussion

Local variation in pre-fire fuel loads significantly affected post-fire resprouting of groundcover shrubs at a scale of $1m^2$ in a frequently burned longleaf pine savanna. The increases in maximum fire temperature and heat output that occurred in areas with added fuels, particularly wood (Chapter 2), decreased shrub resprouting and increased the probability that species would be eliminated from subplots. However, reduction of fire temperature by fuel removal, as much as several hundred degrees below that of unaltered fuels, did not affect resprouting. These results support the "ambient temperature" hypothesis and other studies in longleaf pine savannas that have linked increased mortality of savanna trees with areas of high fire intensity near large pines (Rebertus et al. 1989b, a, Glitzenstein et al. 1995). Conversely, my results differ from previous studies of groundcover shrub communities that have found only limited evidence of fire intensity effects on shrub resprouting (Olson and Platt 1995, Drewa et al. 2002).

Fire intensity effects on groundcover shrubs may only be evident locally and at very high fire intensity. Studies that have found negative effects on shrub resprouting in other community types (Moreno and Oechel 1991, Drewa 2003) have manipulated fuel loads to produce high fire intensities. In frequently burned savannas, these heavy fuel loads tend to occur only in local areas; usually associated with areas of heavy needle or branch fall near large trees (Herman 1993). Studies that have measured fire temperatures within plots without manipulating fuels (Olson and Platt 1995, Drewa et al. 2002) may not have sampled areas with fuel loads heavy enough to reduce shrub densities. Effects on trees (stems > 2 cm dbh) observed where fuels were not experimentally manipulated (Williamson and Black 1981, Rebertus et al. 1989b, a, Platt et al. 1991) may be a result of these species being more

susceptible than shrubs to high fire intensity. Trees may be less capable of resprouting after high intensity fires as a result of senescence of dormant buds, development of apical dominance that inhibits lateral growth, and allocation of stored carbohydrate to aboveground structures (Drewa et al. 2002). Conversely, pine savanna groundcover shrubs resprout quickly from large numbers of dormant buds following fires (Olson and Platt 1995). These shrubs often produce large genets capable of mobilizing stored reserves over many square meters, potentially limiting their susceptibility to the effects of fire intensity (Matlack 1997). Furthermore, fire intensity effects on shrubs may not be evident below some threshold temperature or intensity. For example, fuel removal decreased fire temperature nearly 400ºC, on average, below that of unaltered fuels, but had no effect on resprouting.

Fuel load effects on shrubs may differ among fires as a result of weather patterns prior to fires. Fuel addition, particularly of wood, produced significantly greater effects on shrub resprouting and genet mortality in 1999 fires than 2001 fires. Pre-fire weather conditions in 1999 allowed fuels to dry more completely than in 2001, resulting in higher levels of fuel consumption and heat output (Chapter 2). However, maximum fire temperatures did not decrease significantly from 1999 to 2001. This suggests that fuel load variation interacts with weather conditions to produce local patterns of fuel consumption that affect shrub resprouting and mortality. Similar effects of fuel moisture and fuel amount have been demonstrated in fires in mesquite savannas (Ansley et al. 1998). Furthermore, fire effects on shrubs may be more related to the amount of fuels consumed during a fire than to the maximum fire temperature. This may also partially account for the limited evidence of a relationship between shrub resprouting and maximum fire temperature observed in previous studies (Olson and Platt 1995, Drewa et al. 2002).

High local intensities within single fires do not appear to produce differences in resprouting responses among groups of species (both native and non-native). Addition of fuels reduced resprouting of native rhizome species and non-native species more than that of root crown species. However, overall density of rhizomatous species increased over the course of the study, while density of root crown and non-native species tended to not change or even decrease. These results suggest that repeated growing season fires are affecting rhizomatous species in ways not directly related to fire intensity. Many rhizomatous pine savanna shrubs produce large numbers of interconnected ramets along rhizomes or runners > 1m in length (Olson 1992). Furthermore, some common rhizomatous shrubs, particularly *Rhus copallinum*, produce large numbers of resprouts in the first two months following fires (Olson and Platt 1995, J. Thaxton *pers. obs.*). These life-history characteristics may allow rhizomatous species to take advantage of the open spaces and micro-environmental heterogeneity produced by growing season fires. In contrast resprouting of some root crown and non-native species, particularly *Ilex vomitoria* and *Ligustrum sinense*, was delayed by fires. Furthermore, resprouting of *Ligustrum sinense* along runners appeared to be delayed until the second year following fire (J. Thaxton, *pers. obs.*).

Decreased average height of resprouts within the groundcover shrub community may be related to overall production of shorter ramets, as well as an increase in the relative abundance of small-stature rhizomatous species. Resprouting shrubs in fire-frequented communities store carbohydrate in underground storage organs (Bowen and Pate 1993, Matlack 1997). After removal of aboveground parts by fire, carbohydrate is then mobilized to resprouting stems (Bowen and Pate 1993, Matlack 1997). Thus along with a reduction in number of resprouts as a result of damage to dormant buds, high fire intensity may reduce a

plant's ability to produce large sprouts by damaging storage organs and the ability to relocate stored resources. Also, the overall reduction in resprout height may be related to increases in the relative abundance of rhizomatous species such as *Gaylussacia dumosa* and *Rhus copallinum*. Both species nearly doubled in abundance over the course of the study and produced large numbers of small (<30 cm) ramets.

Elevation effects on resprouting and species loss reflected initial differences in species abundance across topographic gradients. Exotic species, specifically *Ligustrum sinense*, made up nearly 50% of stems at low elevations. Many of these shrubs were large (1.5-3 m height) and had not been topkilled by previous fires (W.J. Platt, *pers. obs.*). High probabilities of species loss in wood addition plots at low elevations, suggests that genets of these shrubs were particularly susceptible to hot fires. Furthermore, probabilities of species loss were highest following the first fire suggesting that these large individuals might have been limited in their ability to resprout, potentially as a result of senescence of dormant buds (Bosela and Ewers 1997).

Results of my study suggest that small-scale variation in fuel loads may increase the heterogeneity and diversity of pine savanna groundcover. Alteration of natural fire regimes, through fire suppression and dormant season burning, has resulted in increased shrub densities in many pine savannas (Platt and Schwartz 1990, Glitzenstein et al. 1995, Gilliam and Platt 1999, Drewa et al. 2002). The reintroduction of frequent growing season burns into these communities appears to limit further encroachment, but does not significantly reduce shrub densities (Olson and Platt 1995, Drewa et al. 2003). Most fires in pine savannas, even when occurring under dry conditions during the growing season, do not reach intensities that eliminate shrubs over large areas. My results suggest that shrub populations are severely

affected only in relatively small areas with extremely heavy fuels. In these areas shrub mortality can be substantial, with the number and size of post-fire resprouts reduced relative to other areas within the same fire. These local "hotspots" may produce open spaces with reduced competition that provide establishments opportunities for forbs and grasses, thereby enhancing local species diversity.

CHAPTER 4

EFFECTS OF FIRE INTENSITY ON THE DEMOGRAPHY OF A RHIZOMATOUS SHRUB, *RHUS COPALLINUM* (ANACARDIACEAE)

Introduction

Fires affect plant population growth rates by altering vital rates associated with survival, growth, and fecundity. By decreasing growth or survival of seeds, seedlings or reproductive adults, fires may decrease fecundity and potentially limit population growth (Hoffmann 1998, 1999, Garnier and Dajoz 2001). Conversely, fires may increase reproductive output in some populations by stimulating flowering of surviving adults (Abrahamson 1984, Brewer and Platt 1994a) or germination of dormant seeds (Keeley 1987, Spier and Snyder 1998). In frequently-burned savannas, individual fires kill few established plants, but may decrease the size or fecundity of survivors (Hoffmann 1998, Hoffmann and Solbrig 2003). However, decreases in reproductive output as a result of fire may be accompanied by increased allocation to clonal growth (Matlack et al. 1993, Hoffmann 1998). For example, many shrubs tend to be top-killed by fire but resprout from dormant buds along underground storage organs (Moreno and Oechel 1993, Olson and Platt 1995, Drewa et al. 2002, Hoffmann and Solbrig 2003). Furthermore, fires may affect the structure of clones and increase their ability to spread laterally and produce clonal sprouts (Brewer and Platt 1994b, Hoffmann 1999). Thus, fires influence vital rates through potentially interactive effects at all life-cycle stages. Analysis of fire effects on populations should benefit from study of the contributions of fire to components of demography at all life-cycle stages.

Stage-structured matrix models (Caswell 2001) have indicated that frequent fires result in population growth for some species and decline for others. Annual fires positively affect population growth of a dominant South American savanna grass (Silva et al. 1991), but reduce population growth of an African savanna grass (Garnier and Dajoz 2001). Stochastic and periodic models of fire frequency effects on an endangered prairie herb indicate that

higher fire frequency decreases extinction probability and increases the importance of seedlings to population growth (Kaye et al. 2001). Matrix models of populations of woody species have indicated that very frequent fires are likely to result in decreasing populations (Price and Bowman 1994, Hoffmann 1999). These models predict significant effects of altered fire frequency, but in all cases fire has been treated as an event with uniform effects across populations. Demographic patterns and model predictions may not be constant across populations if fire intensity varies within single fires.

Fires of variable intensity may produce demographic variability within and among plant populations. In frequently burned plant communities, small-scale variation in fire intensity and behavior within single fires is largely a result of local differences in the amount of fuel (fuel load) available to fires (Odion and Davis 2000, Molina and Llinares 2001). In longleaf pine savannas high fire intensity, resulting either from accumulation of pine needles (Williamson and Black 1981, Platt et al. 1991) or coarse woody debris (Chapter 2), reduces the survival and resprouting of some species (Williamson and Black 1981, Rebertus et al. 1989, Chapter 3). In some cases, particularly heavy fuel loads may result in hotspots, small areas where fires are intense enough to eliminate all or nearly all established plants (Hermann 1993, Brewer et al. 1996). Such hotspots may provide opportunities for the establishment of new individuals either by seedling establishment or clonal growth.

I developed a stage-based matrix model to examine the effects of local fire intensity on a rhizomatous shrub, *Rhus copallinum*, in a frequently burned longleaf pine savanna. I used a ramet-based model to project population growth for ramets in "subpopulations" that burn at different intensities during fires. Ramets were sampled within small ($1m^2$) areas where pre-fire fuels were manipulated to alter local fire intensity. I used annual and 3-year

periodic matrices to assess the effects of fuel treatments (through effects on fire intensity) on asymptotic population growth rates. Each periodic matrix projected the subpopulation through a sequence of one fire year and two post-fire years; this three-year sequence was assumed to occur repetitively. I use elasticity analysis to develop hypotheses regarding those life cycle stages most affected by fire intensity. Three questions are asked in this study: 1) Does fuel load affect the fate of ramets? 2) Does fuel load affect projected population growth? 3) Does fuel load affect the relative importance of different life cycle stages to population growth? My *a priori* expectations were that addition of fuels would result in increased mortality of ramets, thereby reducing population growth. Furthermore, I expected that fuel addition would increase the relative importance of large ramets to population growth because of size-specific patterns of clonal ramet production.

Methods

Study Species and Site

This study was conducted in frequently burned upland longleaf pine savannas at Camp Whispering Pines (30º41'N: 90º29'W), Tangipahoa Parish in eastern Louisiana. Camp Whispering Pines (hereafter CWP) contains second-growth longleaf pine savannas that regenerated naturally following logging in the 1930's. All pine savannas at CWP have been burned biennially during late spring or early summer for the past decade. The groundcover contains a highly diverse assemblage of shrubs, grasses and forbs and is similar to that of other frequently burned longleaf pine savannas along the Gulf coastal plain. More information on the flora and history of CWP is available elsewhere (Noel et al. 1998, Chapter 3).

In this study, I utilized experimental subplots established as a part of a multi-year study of fire effects on shrubs at CWP. In 1998, a total of 540 $1m^2$ subplots were established to investigate the effects of fuel load manipulation on fire intensity and shrub resprouting. Subplots were located within larger plots (n=20) nested within ravines across topographic gradients. Shrub stem density was determined annually in each subplot for five years (1998-2002). Prior to prescribed fires in spring of 1999 and 2001, each subplot was randomly assigned one of four fuel load treatments: unaltered control, fine fuel removal, pine needle addition or wood addition. Fuel load treatments mimicked the natural variation in fuel loads occurring in frequently burned pine savannas. In each fire, addition of either pine needle or woody fuels increased fire intensity relative to unaltered controls, while removal of fine fuels decreased fire intensity relative to controls (Chapter 2). Altered fire intensity produced by fuel load treatments affected shrub survival and resprouting after fires. Fuel addition (both pine needles and wood) increased shrub mortality and decreased resprouting relative to unaltered controls and fine fuel removals (Chapter 3).

Rhus copallinum L. (Anacardiaceae), flameleaf sumac, is a common shrub of southeastern longleaf pine savannas (Olson and Platt 1995, Carter et al. 1999). This species is the most abundant shrub in subplots at Camp Whispering Pines. Clones form along underground rhizomes that may reach several meters in length. Ramets are top-killed by frequent growing season fires, but typically resprout with < 2 weeks. Resprouting can occur both at the base of dead stems as well as from other points along the rhizome. Thus clonal production of new ramets can potentially occur at the location of pre-fire ramets as well as away from pre-fire ramets. Top-killed ramets are capable of resprouting and flowering within

3 months after fire. Fruits mature in the late summer and early fall and may remain on the plants throughout the winter (J. Thaxton, *per obs.*).

Demographic Data

Demography of *R. copallinum* ramets was monitored over three years in a random sample of $1m^2$ subplots. During summer 2000, one year prior to fires, ramets were present in 304 of the 540 subplots from the larger study. At this time, all *R. copallinum* ramets were tagged within 80 of these subplots (n=20 for each fuel load treatment). All subplots received fuel load treatments as part of the larger study (Chapter 2, 3) and were burned during the spring of 2001. A second census occurred 2 months post-fire in June 2001 and subsequent censuses occurred annually until 2003. At each census, mortality of previously tagged ramets was recorded and height of all surviving ramets was measured. New stems were tagged, measured for height and identified as either seedlings or resprouts from rhizomes. Ramets in the 2001 census were resprouts because all ramets were top-killed by fire in spring 2001. If resprouts appeared at a location basal to a dead pre-fire stem they were considered to be the same stem and retained the same tag number in the census. Other resprouts, both in fire and non-fire years, emanated from rhizomes at some distance away from either dead or live stems. These resprouts were considered new clonal ramets. During each census the number of flowers or fruits per reproductive ramet was recorded. To analyze fuel effects on population dynamics, groups of subplots that received a particular fuel load treatment were considered separate subpopulations.

Limited demographic data on seeds and seedlings were generated from germination and transplant experiments. More than 2,000 seeds were collected from 18 reproductive plants at CWP during the fall of 2001. All seeds were collected from plants outside of

subplots. During March 2002, 400 seeds were placed in wire pouches (n=20 seeds per pouch) and placed in the field. After 2 months, seeds were retrieved and germinated either without further treatment (n=100) or after soaking with H_2S0_4 (n=300). All seeds were germinated on a peat moss based germination medium in climate-controlled greenhouses. Percent germination was recorded daily for 2 months.

Seedling growth and survival were examined using transplant experiments in treated subplots after fire. Seedlings were germinated from seeds collected from the field in fall 2001. Seeds treated with H_2S0_4 germinated within two weeks under greenhouse conditions. A total of 324 seedlings were transplanted into the field in May 2002, approximately one month after germination. Seedlings were transplanted into $1m^2$ subplots from the previous study of fire intensity and shrub resprouting. All subplots had received fuel load treatments prior to fires in 1999 and 2001. One seedling was transplanted into the middle of each subplot (n=96 subplots for pine needle addition, fuel removal and controls, n=36 for wood addition). Seedlings were censused for growth and mortality 2 weeks after planting and after one year.

Demographic Patterns and Analyses

Stage classification: A life-cycle graph was generated for *R. copallinum* on the basis of life-history stages and ramet height (Figure 4.1). Stages of established ramets are based on size: small (<10 cm), medium (10-<30 cm) and large (>30). Established ramets can move to a larger size class (growth), remain in the same size class (stasis) or move to smaller size class (regression) within each year. New individuals are assumed to enter the population as either seedlings formed by sexual reproduction or new ramets formed by clonal growth. Only large ramets produced seeds, but ramets in all size stages produced clonal sprouts. New clonal

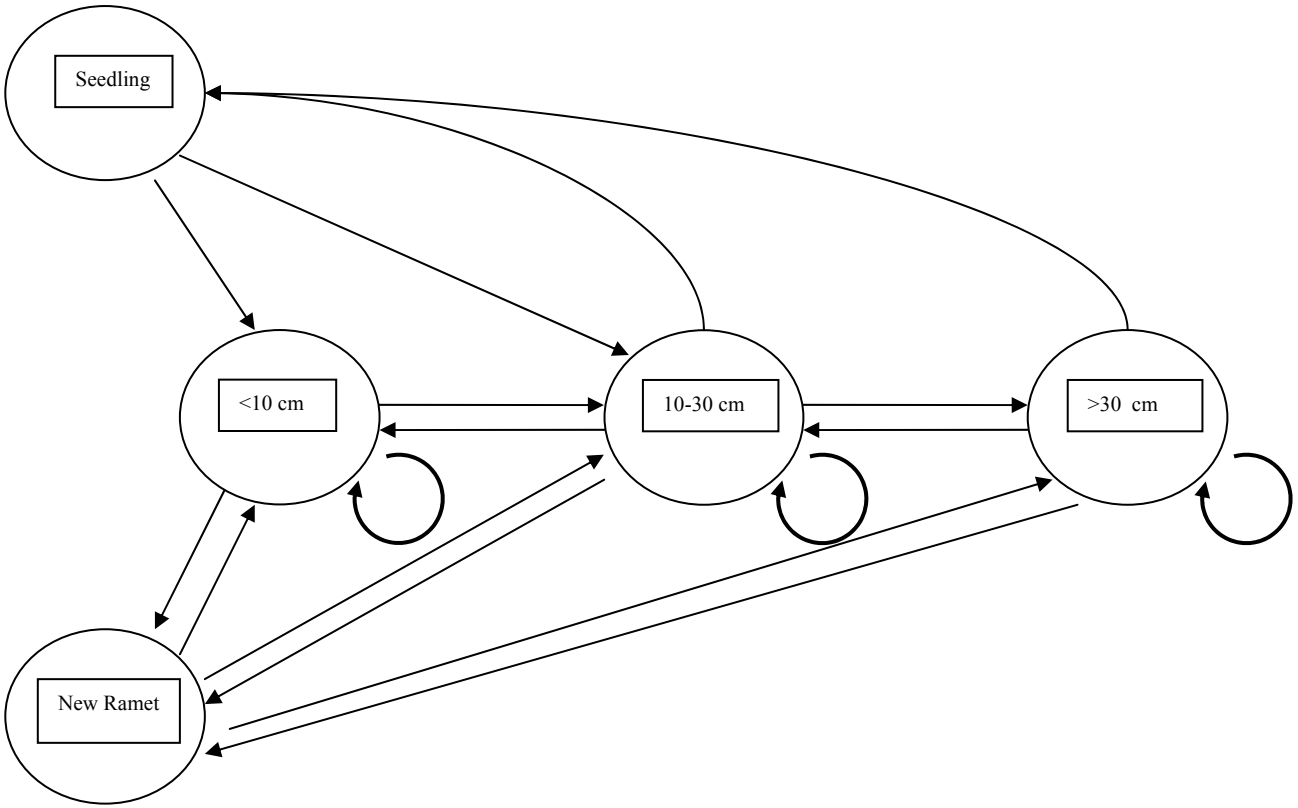


Figure 4.1 Life cycle of *Rhus copallina* in frequently burned longleaf pine savanna. Arrows indicate all possible transitions resulting from stasis, growth, regression, clonal growth and fecundity.

ramets could enter the population at any size stage, but seedlings entered established ramet stages as either small or medium ramets.

Fates of ramets and seedlings: Log-linear analyses were used to assess the effects of fuel load treatments and years on fates of ramets in each stage. At each census, ramets could experience one of four fates: death, stasis, growth or regression. A null model predicting that the fate *F* of each ramet was independent of fuel treatment *T* and year *Y,* given a preset fuel by year interaction, was constructed and denoted as (TY, F). An equation for the null model is the following: $\log m_{ijk} = \mu + \mu_{T(i)} + \mu_{Y(j)} + \mu_{F(k)} + \mu_{RY(ij)}$. The effect of fuel treatment on fate was tested by fitting a model that included a fuel treatment by fate interaction (TY, TF) and comparing its fit to the null model. The effect of year on fate was tested similarly by fitting a model that included a year by treatment interaction (TY, YF) and comparing it to the null model. Model comparisons were made by calculating a change in G^2 statistics between models and comparing these values to a χ^2 statistic with appropriate degrees of freedom. Log-linear analyses were conducted using PROC GENMOD in SAS (SAS Institute 1997).

Survival probability of seedlings was analyzed by mixed model logistic regression. A model was constructed with a logit link and binomial error distribution to test the effects of fuel load treatment, elevation and initial height on probability of seedling survival to one year. Fuel load treatment and elevation (high or low) were considered fixed effects while variation among ravines and subplots was considered to be random. Initial seedling height was used as a covariate in all analyses. To account for the effects of initial transplant shock on survival, seedlings that died within the first 2 weeks after transplanting were removed from this analysis. Analyses were conducted by invoking PROC MIXED within the GLIMMIX macro (Littell et al. 1996) in SAS (SAS Institute 1997).

Clonal ramet production: Repeated measures ANCOVA was used to test for effects of fuel load treatment on production of clonal ramets over three years. Density of new clonal ramets was determined annually in all $1m^2$ subplots (n=80). Density data were natural log-transformed and analyzed as a split-plot model using PROC MIXED in SAS (SAS Institute 1997). Fixed effects included fuel treatment and year while variation among $1m^2$ subplots was random. Fuel effects were tested over the whole plot error (variation among subplots within fuel treatments), while year effects were tested over the residual error. Initial density of established ramets and elevation of each subplot were used as covariates. The best fit to the model was provided by a first order autoregressive variance-covariance structure. Comparisons among treatment means were made using *a priori* linear contrasts.

Periodic Matrix Models

Construction of matrices: A total of 24 projection matrices were constructed to model population dynamics of *R. copallinum* (Table A.1, Appendix). Matrix elements (a_{ij}) indicate the probability of an individual of stage *j* at time *t* moving to stage *i* at time *t+1*. All subplots receiving the same fuel load treatment prior to fires were treated as a subpopulation, resulting in four subpopulations and four sets of annual matrices. Each set of matrices per subpopulation consisted of 2 sequential matrices per year for each of 3 years (Table 4.1). Each of the three years represented a unique set of environmental conditions: fire year, one year post-fire and two years post-fire. Some transitions did not occur in all years. For example, plants did not produce seeds that developed into seedlings during the fire year. During both post-fire years, plants produced seeds that could potentially result in established seedlings. During the second year post-fire, seedlings produced by seeds in the previous year recruited into established ramet size classes.

Table 4.1 Generalized stage-structured projection matrices ($\mathbf{B}_{ia}$ and $\mathbf{B}_{ib}$) for *Rhus copallinum* in frequently burned pine savanna at Camp Whispering Pines. Matrix entries include transition probabilities associated with stasis (S), growth (G), regression (R), fecundity (F) and clonal growth (CG). Two matrices are used in each year to incorporate the production of new clonal ramets and their immediate recruitment into established ramet size classes.

Fire year (2000-2001)			***Stage at time t***		
(B_{1a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	CG_{24}	CG_{25}
Small ramet (<10cm)	0	0	S_{33}	R_{34}	R_{35}
Medium ramet (10-30cm)	0	0	G_{43}	S_{44}	R_{45}
Large ramet (>30cm)	0	0	0	G_{54}	S_{55}
(B_{1b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	G_{32}	1	0	0
Medium ramet (10-30cm)	0	G_{42}	0	1	0
Large ramet (>30cm)	0	G_{52}	0	0	1

1 yr. post-fire (2001-2002)			***Stage at time t***		
(B_{2a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	F_{15}
Clonal ramet (new)	0	0	0	CG_{24}	CG_{25}
Small ramet (<10cm)	0	0	S_{33}	R_{34}	0
Medium ramet (10-30cm)	0	0	G_{43}	S_{44}	R_{45}
Large ramet (>30cm)	0	0	G_{53}	G_{54}	S_{55}
(B_{2b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	G_{32}	1	0	0
Medium ramet (10-30cm)	0	G_{42}	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Table 4.1 continued

2 yrs. post-fire (B_{3a})	***Stage at time t***				
(B_{3a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	F_{15}
Clonal ramet (new)	0	0	0	CG_{24}	CG_{25}
Small ramet (<10cm)	G_{31}	0	S_{33}	R_{34}	0
Medium ramet (10-30cm)	G_{41}	0	G_{43}	S_{44}	R_{45}
Large ramet (>30cm)	0	0	0	G_{54}	R_{55}
(B_{3b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	G_{32}	1	0	0
Medium ramet (10-30cm)	0	G_{42}	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Two sequential matrices were used in each year to incorporate the formation of new ramets through clonal growth and their immediate entrance into established ramet size classes (Table 4.1). The first matrix ($\mathbf{B}_{ia}$) contains both stage specific sexual reproduction (top row) and production of new clonal ramets (second row) as forms of fecundity. Other entries in the matrix are probabilities of stasis (diagonal), growth (below diagonal) and retrogression (above diagonal) for established ramets. The second matrix ($\mathbf{B}_{ib}$) incorporates new clonal ramets produced in the first matrix into established ramet size classes with a column vector for growth of new ramets. All other entries remain unchanged by entering 1's along the main diagonal. The product of these two matrices takes the form:

$$n_{(t+1)} = [\mathbf{B}_{ib}\mathbf{B}_{ia}]n_{(t)} = \mathbf{B}_1 n_{(t),}$$

where $\mathbf{B}_1$ is a matrix product describing the composite transition probabilities over one year (Table A.2, Appendix). $\mathbf{B}_i$ matrices are hereafter called annual matrices and are available in the Appendix (Table A.2). In all $\mathbf{B}_i$ matrices, both column and row vectors associated with the production and growth of new clonal ramets are zero. This is because all clonal ramets are recruited into established ramet size classes in the year they are produced.

I initially examined the effects of fuel treatments and years on the projected asymptotic population growth rate, λ, of each annual matrix. Lambda is calculated as the dominant eigenvalue of each matrix (Caswell 2001). A value of $\lambda > 1$ indicates that the population is growing, and $\lambda < 1$ indicates that the population is decreasing. When $\lambda = 1$ the population is predicted neither to increase nor to decrease. An estimate of the variance of λ was generated using the method described by Lande (1988). An approximation to the variance of λ is described by:

$$V(\lambda) \approx \mathbf{\Sigma} \, (\partial \lambda / \partial a_{ij})^2 \, V(a_{ij})$$

where ($\partial\lambda/\partial a_{ij}$) is the sensitivity of λ to a change in any matrix element, a_{ij}, and $V(a_{ij})$ is the sample variance of each matrix element. The variance estimate was used to generate approximate 95% confidence intervals for λ. When confidence intervals did not overlap, differences in λ were considered significant. Finally, the proportional effect on λ of a perturbation in matrix elements was examined by generating an elasticity matrix for each annual matrix.

A periodic matrix was constructed to project each *R. copallinum* subpopulation over the entire 3-year cycle a fire year followed by two non-fire years. The projection matrix is the following:

$$n_{(t+3)} = [\mathbf{B}_3\, \mathbf{B}_2\mathbf{B}_1\,]n_{(t)} = \mathbf{A}_1 n_{(t),}$$

where the composite matrix for each transition year is indicated by $\mathbf{B}_i$ and for the entire projection by $\mathbf{A}_{\underline{i}}$**.** The subscript for **B** indicates its year in the sequential set of matrices and the subscript for **A** indicates the year in which the projection begins. The dominant eigenvalue of $\mathbf{A}_i$ provides the asymptotic population growth rate, λ, over the projection interval. The mean annual finite rate of increase is obtained by raising the dominant eigenvalue of $\mathbf{A}_i$ to the inverse of the number of years in the projection interval. All $\mathbf{A}_i$ matrices are available in the Appendix (Table A.3). As for each annual matrix, the elasticity λ to each matrix element was calculated for each **A** matrix. All matrix calculations were performed in MATLAB 6.5.

Estimation of vital rates for matrices: Stage specific rates of clonal ramet production were estimated from clonal ramets that could be linked to parent ramets. For 23% of all new clonal ramets it was possible to identify rhizome connections to nearby established ramets, putative "parents." The size distribution of these clonal ramets was not significantly different

from the size distribution of clonal ramets without parent stems (Kolmogorov-Smirnov test p= 0.80). Therefore this sample of clonal ramets was used to estimate the proportion of new ramets produced by each established ramet size class. Clonal ramets were allocated to established ramet size classes in the following proportion: <10 cm = 0, 10-30 cm = 0.192, >30 cm = 0.808.

Estimates of stage specific fecundity were the probability that a ramet alive at time *t* would contribute a seedling to the population at time *t+1*. These estimates were generated with limited data related to seed production, seed germination and seedling establishment. As an estimate of seed production, the number of flowers per reproductive ramet was determined at each census. Flower production was related to ramet size and was assumed to result in seed production at a ratio of 1:1. A germination percentage (2.0 ± 0.04 %) was estimated as the percentage of untreated seeds collected in fall 2001 that germinated in the greenhouse during summer 2002. This percentage was consistent with the results of a previous study on *R. copallinum* seed germination (Farmer et al. 1982). A seedling establishment probability was estimated as the proportion of planted seedlings that survived for the first 2 weeks in the transplant experiment. The product of seed production, germination probability and establishment probability was used as an estimate of stage specific fecundity. No seed formation occurred during the fire year, so fecundity values are only included in the matrices for one and two years post-fire. Furthermore, it is assumed that as a result of frequent fire there is no long-lived seed bank.

An estimate of seedling survival and growth for each subpopulation was provided by the seedling transplant experiment. Survival probability was estimated as the proportion of seedlings that survived for one year after transplanting in the field. Death of seedlings in the

first 2 weeks after transplanting was included in the probability of establishment, thus one year survival probability was determined only for seedlings that survived at least two weeks. All seedlings that survived for one year were then entered into established ramet size classes. Probability of growth into established ramet size classes was determined on the basis of height at one year.

Results

Effects of Fuel and Year on Stems

Fuel treatments affected the fates of small and large ramets, but not medium ramets or seedlings. Small ramet fates (<10 cm) were dependent on fuel treatment ($p<0.05$, Table 4.2). Based on probabilities from $\mathbf{B}_{ia}$ matrices for each subpopulation, small ramet stasis in control and removal subpopulations tended to be slightly higher than that of pine needle and wood addition subpopulations, particularly during the year of the fire (Table A.1, Appendix). Large ramet fates (>30 cm) also depended on fuel treatment ($p<0.05$, Table 4.2). Fuel effects on large ramets were most evident during the year of the fire, where large ramet stasis was 30% in the control subpopulation, < 20% in removals and <10% in both fuel addition subpopulations. Fuel treatments did not affect fates of either medium ramets (10-30 cm) nor seedlings. After adjusting for a significant effect of initial height ($p=0.04$, Table 4.3), the probability of seedling survival for one year averaged >70% across all fuel treatments.

Fates of both medium and large ramets differed between fire and non-fire years. Fates of medium ramets (10-30 cm) were dependent on year ($p<0.001$, Table 4.2). Growth of medium ramets into the large ramet size class averaged slightly more than 20% in non-fire years over all subpopulations but was nearly zero in fire years. Stasis of medium ramets tended to be 30-50% in both fire and non-fire years. Fates of large ramets were also

Table 4.2 Log-linear analyses of the effects of fuel treatment and year on fate of ramets within each initial stage. G^2 statistics indicate the difference in fit between the null model and a model containing either the interaction of fate by year or fate by treatment. Significance was determined by comparing the test statistic to the critical value for a χ^2 distribution with appropriate degrees of freedom (df_{fuel}=9, df_{year}=6).

	Fuel Trt		Year	
Ramet Stage	G^2	**p-value**	G^2	**p-value**
Small (<10 cm)	17.697	<0.05	10.988	*ns*
Medium (10-30 cm)	13.560	*ns*	132.189	<0.001
Large (>30 cm)	20.077	<0.05	157.784	<0.001

ns= not significant (p-value > 0.05)

Table 4.3 Results of generalized linear mixed model analysis of fuel and elevation effects on seedling survival. Initial height served as a covariate. Error term for Elevation = Elevation x Transect; Error term for Fuel and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Covariate (Initial Height)	1	114	4.18	0.04	*
Elevation	1	9.87	1.4	0.26	
Fuel	3	282	0.4	0.75	
Elevation x Fuel	3	282	0.28	0.84	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	282	0.62	0.43	
Removal x (Needle Addition + Wood Addition)	1	282	0.75	0.39	
Needle Addition + Wood Addition	1	282	0.23	0.63	

dependent on year ($p<0.001$). Approximately 50% of the large ramets at the time of fire (in each subpopulation) regressed to the medium size class after fire because resprouting stems did not attain pre-fire stem sizes.

Patterns to the production of clonal ramets differed among years. After adjusting for a significant effect of initial density of established ramets ($p<0.001$, Table 4.4), overall production of new clonal ramets during the fire year (2001) was more than twice that of either post-fire year (Figure 4.2). The overall effect of year was significant ($p<0.0001$). Linear contrasts also indicated significant differences between the fire year and both post-fire years ($p<0.0001$), as well as between the two post-fire years ($p=0.002$). Neither the overall effect of fuel ($p=0.98$), nor the effect of fuel by year interaction ($p=0.46$) was significant.

Population Growth and Elasticity

Among fuel load treatments, fuel addition had the largest effect on asymptotic population growth rates (λ) determined from annual (B_i) matrices (Figure 4.3). During the fire year, λ for the pine needle addition subpopulation was 0.62, significantly less than that of the control subpopulation. During the first year post-fire, the pattern was reversed with λ for the pine needle addition subpopulation significantly greater than that of either control or fuel removal subpopulations. In both of these years, λ for pine needle addition was significantly different from 1. Similar to pine needle addition, λ for the wood addition subpopulation tended to be less than that of control and fuel removal in the fire year and greater than control and fuel removal during the first year post-fire, but these differences were not significant. The only other subpopulation for which lambda was significantly different from 1 was for the wood addition subpopulation in the second year post-fire.

Table 4.4 Results of mixed model repeated measures ANCOVA of density (natural log transformed) of new clonal ramets. Initial number of established ramets and elevation served as covariates. Error term for Fuel = Subplot(Fuel); Error term for Year and interactions = residual. NDF=numerator degrees of freedom; DDF=denominator degrees of freedom based on Satterthwaite approximation. Covariance structure for Subplots(Fuel) = 1st order autoregressive.

Source of Variation	NDF	DDF	F	*p*	
Fixed Effects:					
Covariate (Initial Ht.)	1	71	14.03	0.0004	*
Covariate (Elevation)	1	71	0.58	0.449	
Fuel	3	71	0.06	0.978	
Year	2	146	79.85	<0.0001	*
Fuel x Year	6	146	0.95	0.46	
Linear Contrasts (Fuel):					
Control x (Removal + Needle Addition + Wood Addition)	1	71	0.02	0.891	
Removal x (Needle Addition + Wood Addition)	1	71	0.09	0.763	
Needle Addition + Wood Addition	1	71	0.08	0.781	
Linear Contrasts (Year):					
fire year x (post-fire1 + post-fire2)	1	146	149.79	<0.0001	*
post-fire 1 x post-fire 2	1	146	10.42	0.0015	*

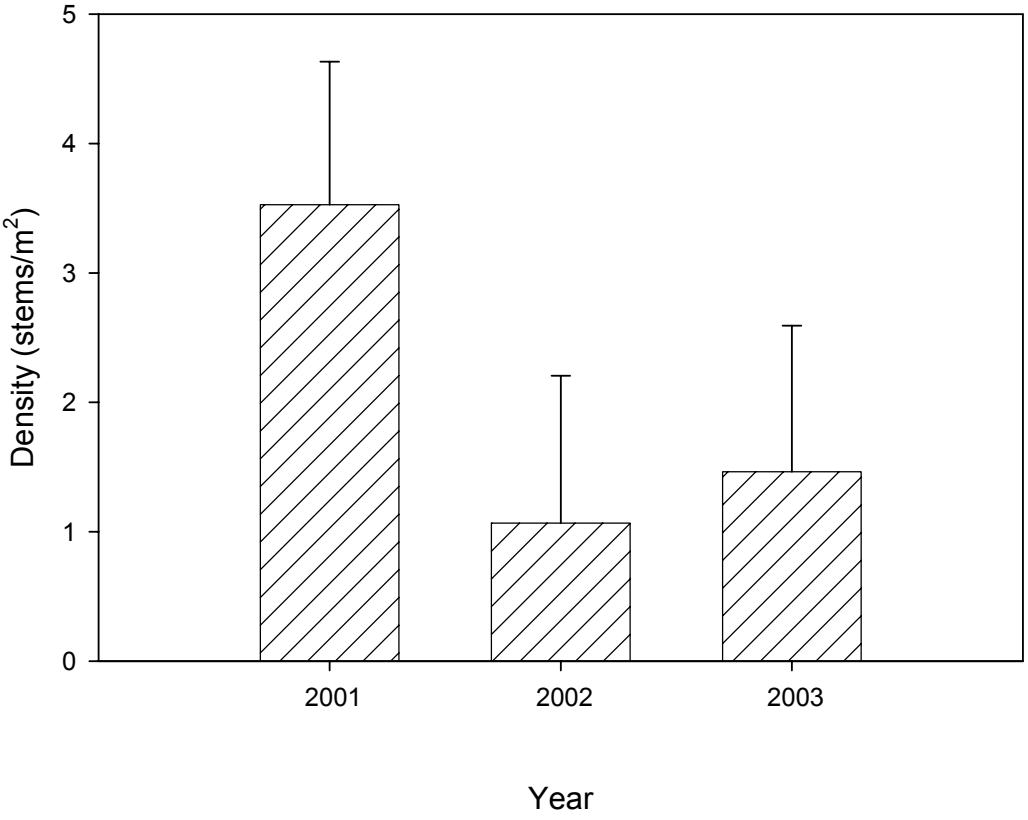


Figure 4.2 Mean density of new clonal ramets in subplots in each year. Bars indicate back-transformed least squares means with 95% confidence intervals.

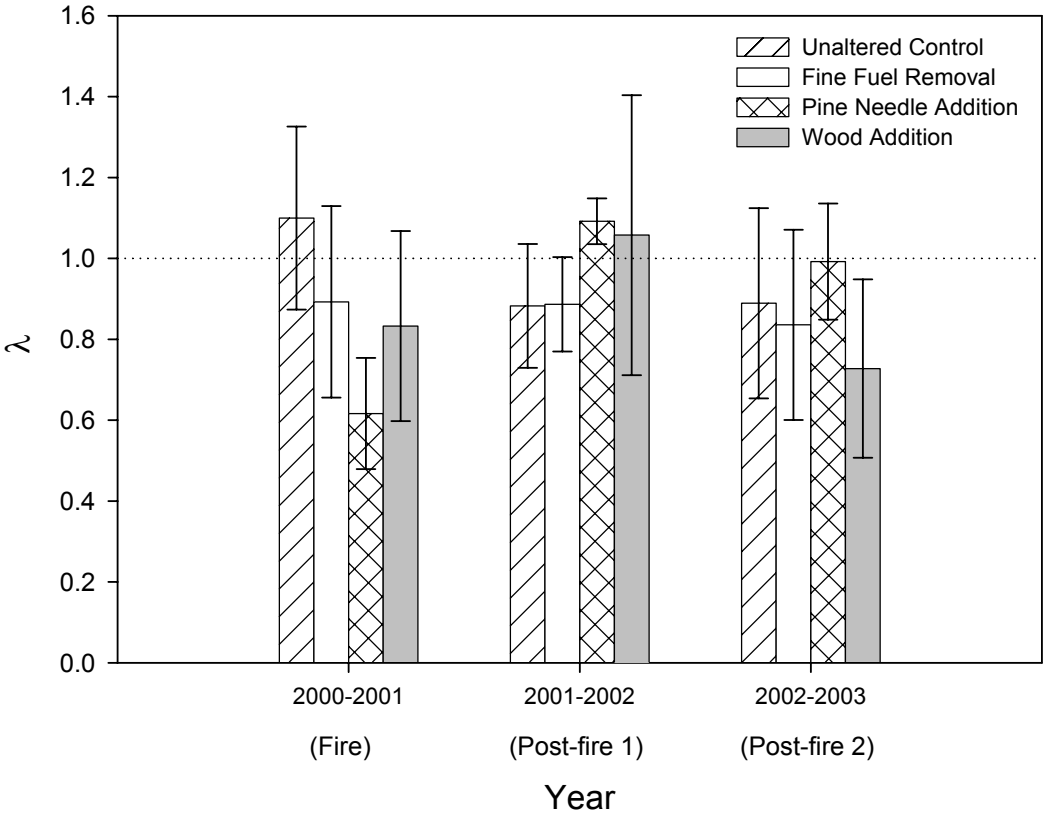


Figure 4.3 Asymptotic population growth rates for populations receiving one of four fuel load treatments (control, fuel removal, pine needle addition, or wood addition) prior to fire in 2001. Error bars indicate approximate 95% confidence intervals.

The asymptotic population growth rates indicated by the 3-year periodic matrix ($\mathbf{A}_1$) indicated that control and pine needle addition subpopulations were increasing while fuel removal and wood addition subpopulations were decreasing. Over one cycle of a fire in year one, followed by two non-fire years, the control subpopulation was predicted to increase (λ=1.08) while the pine needle subpopulation was nearly stable (λ=1.01). Both the fuel removal subpopulation (λ=0.92) and wood addition subpopulations were decreasing (λ=0.77).

Elasticity matrices generated from the 3-year periodic matrices indicated that transitions in the largest size classes in all four subpopulations have the largest effect on λ over periods that involve both fire and non-fire years (Figure 4.4). Transitions associated with stasis within the two largest size classes, as well as growth into and regression out of the largest size class had proportionally the largest effects on lambda. These four transitions (bars in the bottom right corner of each panel) together accounted for approximately 70% of the total elasticity in the pine needle addition subpopulation and approximately 90% for control, removal and wood addition subpopulations. Stasis within the largest size class alone accounted for approximately 1/3 of the total elasticity for each subpopulation. Patterns were consistent across subpopulations. There is no elasticity associated with fecundity in these matrices because all seedlings alive in the 3rd year of each cycle either die or are recruited into established ramet size classes. Seeds produced in the 3rd year of each cycle are assumed killed by fire, thus they do not produce seedlings.

Discussion

Population growth rate of *R. copallinum* in a frequently burned longleaf pine savanna is largely determined by the probabilities of stasis among larger ramets. In all subpopulations the survival of large ramets was the primary determinant of population growth. In frequently

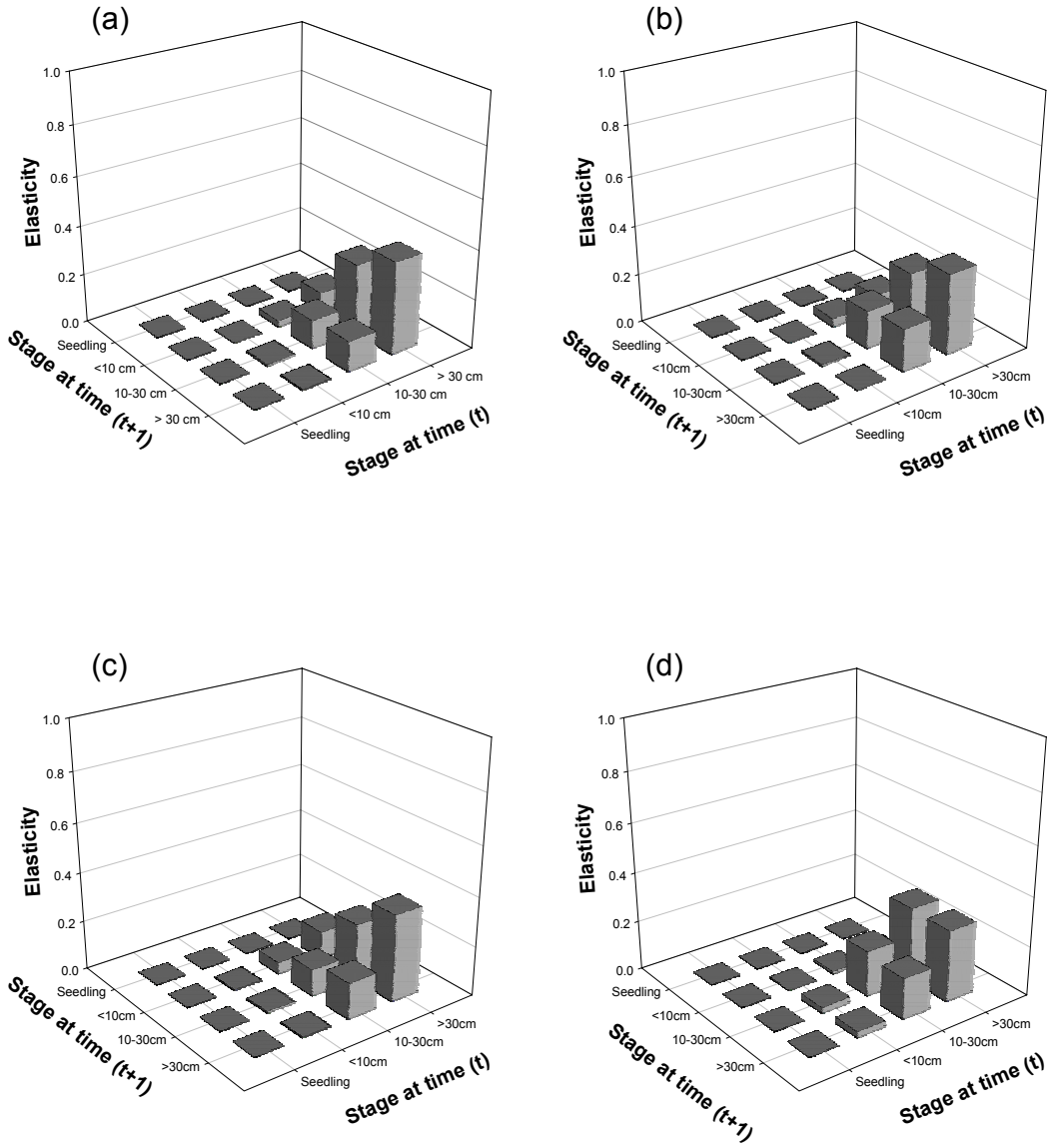


Figure 4.4 Elasticity values for 3-year periodic matrices for each population: (a) control (b) fine fuel removal, (c)pine needle addition and (d) wood addition.

burned populations of *R. copallinum,* stasis within ramet stages and positive population growth is maintained by the production of new ramets that are capable initially of rapid regrowth after fire and then high survival in non-fire years. High survivorship, particularly of large individuals or ramets, has been shown to be important to population growth of other shrubs (Huenneke and Marks 1987, Hoffmann 1999, Parker 2000). In contrast, burning of some herbaceous species tends to increase the importance of smaller life cycle stages and seedlings to population growth (Silva et al. 1991, Kaye et al. 2001)

Some of the projected differences in population growth among subpopulations may be related to differences in the amount of damage to resprouting organs. I hypothesized that the increased fire intensity produced by both pine needle and wood addition treatments would increase damage to rhizomes, thereby reducing resprouting and increasing the probability of complete kill of genets (Matlack 1997). The decrease in population growth rates in pine needle and wood addition treatments during the year of the fire suggests that fires might decrease initial resprouting . Nonetheless, only the projected three-year population growth of the wood addition subpopulation is <1. This suggests that the initial effect of pine needle addition on *R. copallinum* may be primarily to delay the rate of resprouting. *Rhus copallinum* has been shown to resprout rapidly under a regime of frequent growing season fires (Olson and Platt 1995). Resprout density tends to be highest immediately after fire and then decreases in the years following fire. A delay in resprouting, without significant mortality of genets, could account for the pattern of population growth observed in the pine needle addition subpopulation during the fire year and the first year post-fire. Conversely, absence of significant heating could limit production of resprouts in fine fuel removal subpopulations. Heat stimulated activation of buried buds has been reported for some rhizome resprouting

species (Flinn and Pringle 1983). This may account for the tendency for fuel removal subpopulations to have population growth rates of <1.

Effects of fire intensity on post-fire environmental conditions may interact with damage to resprouting organs to determine patterns of ramet growth and survival. Increased fire intensity resulting from addition of fuels reduces the cover of shrubs and large grasses within an otherwise continuous savanna groundcover (Brewer et al. 1996, J. Thaxton *unpublished data*). Thus rhizomes that survive in these areas of higher fire intensity may produce resprouts that are able to exploit reduced competition. This may result in increased growth and survival of these ramets in the years following fires. Conversely, fuel removal treatments that result in low fire intensity and kill few established genets may be areas where rhizomes are minimally damaged by fires, but then experience intense competition in the following years. This might influence population growth in fuel removal treatment subpopulations. Over longer time scales, the negative effects of fuel removal on ramet survival may be offset by opportunities for sexual reproduction. Areas of reduced fuels and low fire intensity may provide sites where seeds and/or seedlings are capable of surviving fires. This possibility was not included in my model, because I did not generate independent estimates of seed production and germination within treatment subpopulations.

Our results predict different trends for growth of fuel treatment subpopulations over a 3-year cycle of fire followed by two non-fire years. The high value of lambda associated with the control subpopulation suggests that growing season fires of moderate intensity stimulate the ability of *R. copallinum* to resprout and spread clonally in a heterogeneous post-fire environment. In contrast, fuel addition effects may be determined by the extent of damage to rhizomes. When damage results in death of rhizomes and complete kill of individuals (as in

the wood addition subpopulation), then fires are expected to decrease population growth. When fire damage to rhizomes only results in delayed resprouting (as in the pine needle addition subpopulation), the post-fire growth of ramets in an environment of decreased competition is expected to maintain a stable population. Finally, when fuels are removed, population growth is projected to decrease, potentially from reduced resprouting of large ramets and increased competition from neighbors.

The demography of *R. copallinum* within a frequently burned pine savanna may be spatially heterogeneous as a result of local variation in fuels. In this study, population level responses were determined by a complex combination of different demographic responses among subpopulations associated with different types and amounts of fuels**.** Fuel differences were shown to affect many stages of the life cycle, producing a range of different responses that combine to affect subpopulation growth**.** Thus, the demography of *R. copallinum* populations in frequently burned pine savannas should be strongly influenced by fuel characteristics.

CHAPTER 5

CONCLUSIONS

Small-scale differences in fuel loads significantly affect fire intensity and damage to shrubs. Within single fires the amount and type of available fuels was the primary determinant of fire intensity. The addition of pine needle or wood fuels consistently increased the maximum temperature and heat output above that of an unaltered control. Conversely, the removal of fine fuels consistently decreased maximum temperature and heat output below that of an unaltered control. By altering fire intensity, fuel treatments affected the probability of damage to shrubs. Overall, shrub damage was greater in pine needle and wood addition treatments than in control and fuel removal treatments. These results suggest that small-scale variation in fuel loads may be a significant source of environmental heterogeneity within the groundcover of longleaf pine savannas.

Weather conditions prior to fires affect the relationship between fuel loads and fire intensity. During the second year of fires, the average rain-free interval prior to fires was half that of the first year. This resulted in significantly decreased fuel consumption, particularly for wood addition and fine fuel removal treatments. Although differences in fuel consumption between the years had little effect on maximum fire temperature or heat output, there was an effect on the probability of shrub damage. Shrub damage was lower overall during the second year of fires. This suggests that fuel consumption may be the most important characteristic for predicting fire damage to shrubs.

By altering fire intensity, small-scale differences in pre-fire fuels significantly affect shrub resprouting. The addition of fuels, particularly wood, decreased shrub resprouting and increased the probability that species would be eliminated from $1m^2$ subplots. Resprouting and species loss did not differ between control and fuel removal treatments. These results provide support for the "ambient temperature" hypothesis but suggest that fire intensity

effects may only be evident at the highest fire intensities. Heavy fuel loads that produce small areas of high fire intensity significantly affect the post-fire recovery of shrubs, potentially opening space in the groundcover for other species such as grasses and forbs.

Rhizomatous and root-crown species respond similarly to differences in fire intensity. I expected that negative effects of increased fire intensity would be more evident for root crown species than rhizomatous species, but this hypothesis was not supported. High fire intensity reduced rhizomatous resprouting relatively more than that of root-crown species. However, rhizomatous species increased over the course of the study. This result suggests that some effects of frequent growing season fires on the abundance of rhizomatous shrubs are independent of fire intensity.

Fuel treatments affect the demography of *Rhus copallinum*, the most frequently occurring rhizomatous shrub at the study site. Matrix model projections indicated positive population growth of *R. copallinum* in the control treatment and nearly stable populations in the pine needle addition treatment. In contrast, decreasing population growth was predicted for both fine fuel removal and wood addition. In all treatments, the fate of large ramets was most important to population growth. I hypothesize that effects of fuel treatments on population growth of *R. copallinum* result from an interaction of damage to rhizomes with post-fire environmental conditions. Thus population growth increases in areas such as control and pine needle addition treatments where fire intensity is high enough to limit competitors, but not high enough to cause extensive death of genets. These results suggest that the population level responses of *R. copallinum* in a frequently burned savanna may be determined by a complex combination of demographic responses associated with types and amounts of fuels.

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APPENDIX:

MATRICES

Table A.1 All $\mathbf{B}_{ia}$ and $\mathbf{B}_{ib}$ annual matrices used in the study of *Rhus copallina* demography in Chapter 4. Two matrices are used in each year to incorporate the production of new clonal ramets and their immediate transition into established ramet stages. Separate matrices are generated for each subpopulation in each year for a total of 24 matrices.

Control Population

Fire year (2000-2001)			***Stage at time t***		
(B_{1a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	1.126	1.546
Small ramet (<10cm)	0	0	0.50	0.200	0.022
Medium ramet (10-30cm)	0	0	0	0.400	0.543
Large ramet (>30cm)	0	0	0	0	0.30
(B_{1b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.409	1	0	0
Medium ramet (10-30cm)	0	0.557	0	1	0
Large ramet (>30cm)	0	0.034	0	0	1

Control Population

1 yr. post-fire (2001-2002)			***Stage at time t***		
(B_{2a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.188
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.111	0	0
Medium ramet (10-30cm)	0	0	0.156	0.475	0
Large ramet (>30cm)	0	0	0.022	0.388	0.882
(B_{2b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	1	0	0
Medium ramet (10-30cm)	0	0	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Table A.1 continued

Control Population

2 yrs. post-fire (2002-2003)			***Stage at time t***		
(B_{3a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.188
Clonal ramet (new)	0	0	0	0.064	0.258
Small ramet (<10cm)	0.624	0	0	0.044	0
Medium ramet (10-30cm)	0.151	0	0	0.356	0.064
Large ramet (>30cm)	0	0	0	0.089	0.851
(B_{3b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.533	1	0	0
Medium ramet (10-30cm)	0	0.467	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Fine Fuel Removal Population

Fire year (2000-2001)			***Stage at time t***		
(B_{1a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0.960	1.730
Small ramet (<10cm)	0	0	0.300	0.278	0.048
Medium ramet (10-30cm)	0	0	0	0.333	0.500
Large ramet (>30cm)	0	0	0	0.056	0.190
(B_{1b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.556	1	0	0
Medium ramet (10-30cm)	0	0.411	0	1	0
Large ramet (>30cm)	0	0.033	0	0	1

Table A.1 continued

Fine Fuel Removal Population

1 yr. post-fire (2001-2002)			***Stage at time t***		
(B_{2a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.182
Clonal ramet (new)	0	0	0	0.009	0.173
Small ramet (<10cm)	0	0	0.150	0.016	0
Medium ramet (10-30cm)	0	0	0.167	0.344	0
Large ramet (>30cm)	0	0	0.033	0.406	0.786
(B_{2b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.333	1	0	0
Medium ramet (10-30cm)	0	0.667	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Fine Fuel Removal Population

2 yrs. post-fire (2002-2003)			***Stage at time t***		
(B_{3a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.182
Clonal ramet (new)	0	0	0	0.027	0.099
Small ramet (<10cm)	0.645	0	0.083	0	0
Medium ramet (10-30cm)	0.118	0	0.750	0.486	0.049
Large ramet (>30cm)	0	0	0	0.057	0.780
(B_{3b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.40	1	0	0
Medium ramet (10-30cm)	0	0.60	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Table A.1 continued

Pine Needle Addition Population

Fire year (2000-2001)			***Stage at time t***		
(B_{1a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0.440	1.850
Small ramet (<10cm)	0	0	0	0.263	0.026
Medium ramet (10-30cm)	0	0	0	0.342	0.500
Large ramet (>30cm)	0	0	0	0	0.079
(B_{1b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.448	1	0	0
Medium ramet (10-30cm)	0	0.517	0	1	0
Large ramet (>30cm)	0	0.034	0	0	1

Pine Needle Addition Population

1 yr. post-fire (2001-2002)			***Stage at time t***		
(B_{2a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.164
Clonal ramet (new)	0	0	0	0.007	0.404
Small ramet (<10cm)	0	0	0.180	0	0
Medium ramet (10-30cm)	0	0	0.360	0.481	0
Large ramet (>30cm)	0	0	0	0.351	1
(B_{2b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	1	1	0	0
Medium ramet (10-30cm)	0	0	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Table A.1 continued

Pine Needle Addition Population

2 yrs. post-fire (B_{3a})			***Stage at time t***		
(B_{3a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.164
Clonal ramet (new)	0	0	0	0.084	0.588
Small ramet (<10cm)	0.646	0	0.385	0.091	0
Medium ramet (10-30cm)	0.085	0	0.154	0.527	0.030
Large ramet (>30cm)	0	0	0	0.200	0.788
(B_{3b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.583	1	0	0
Medium ramet (10-30cm)	0	0.417	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Wood Addition Population

Fire year (2000-2001)			***Stage at time t***		
(B_{1a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0.612	2.289
Small ramet (<10cm)	0	0	0	0.125	0
Medium ramet (10-30cm)	0	0	0.200	0.313	0.500
Large ramet (>30cm)	0	0	0	0	0.056
(B_{1b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.314	1	0	0
Medium ramet (10-30cm)	0	0.667	0	1	0
Large ramet (>30cm)	0	0.020	0	0	1

Table A.1 continued

Wood Addition Population					
1 yr. post-fire (2001-2002)			***Stage at time t***		
(B_{2a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.166
Clonal ramet (new)	0	0	0	0.004	0.404
Small ramet (<10cm)	0	0	0.111	0	0
Medium ramet (10-30cm)	0	0	0.278	0.551	0
Large ramet (>30cm)	0	0	0	0.245	1
(B_{2b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	1	1	0	0
Medium ramet (10-30cm)	0	0	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Wood Addition Population					
2 yrs. post-fire (B_{3a})			***Stage at time t***		
(B_{3a})	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0.166
Clonal ramet (new)	0	0	0	0.072	0.693
Small ramet (<10cm)	0.548	0	0	0.063	0
Medium ramet (10-30cm)	0.129	0	0	0.406	0.143
Large ramet (>30cm)	0	0	0	0.063	0.643
(B_{3b})					
Stage at time t+1					
Seedling	1	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0.667	1	0	0
Medium ramet (10-30cm)	0	0.333	0	1	0
Large ramet (>30cm)	0	0	0	0	1

Table A.2 Composite annual matrices ($\mathbf{B}_i$) for each treatment subpopulation in the study of *Rhus copallina* in Chapter 4. Each matrix is the product of the $\mathbf{B}_{ia}$ and $\mathbf{B}_{ib}$ matrices for each year. A total of 12 matrices are used to describe population dynamics within 3 subpopulations over 4 years.

Control Population

Fire year (2000-2001)			***Stage at time t***		
(B_1)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.500	0.661	0.654
Medium ramet (10-30cm)	0	0	0.000	1.027	1.404
Large ramet (>30cm)	0	0	0	0.038	0.357
1 yr. post-fire (2001-2002)					
(B_2)					
Stage at time t+1					
Seedling	0	0	0	0	0.188
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.111	0	0
Medium ramet (10-30cm)	0	0	0.156	0.475	0
Large ramet (>30cm)	0	0	0.022	0.388	0.882
2 yrs. post-fire (2002-2003)					
(B_3)					
Stage at time t+1					
Seedling	0	0	0	0	0.188
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0.624	0	0	0.079	0.138
Medium ramet (10-30cm)	0.151	0	0	0.385	0.184
Large ramet (>30cm)	0	0	0	0.089	0.851

Table A.2 continued

Fine Fuel Removal Population

Fire year (2000-2001)			***Stage at time t***		
(B_1)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.300	0.811	1.009
Medium ramet (10-30cm)	0	0	0	0.728	1.211
Large ramet (>30cm)	0	0	0	0.088	0.248
1 yr. post-fire (2001-2002)					
(B_2)					
Stage at time t+1					
Seedling	0	0	0	0	0.182
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.150	0.019	0.058
Medium ramet (10-30cm)	0	0	0.167	0.350	0.115
Large ramet (>30cm)	0	0	0.033	0.406	0.786
2 yrs. post-fire (2002-2003)					
(B_3)					
Stage at time t+1					
Seedling	0	0	0	0	0.182
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0.645	0	0.083	0.011	0.039
Medium ramet (10-30cm)	0.118	0	0.750	0.502	0.108
Large ramet (>30cm)	0	0	0	0.0571	0.780

Table A.2 continued

Pine Needle Addition Population

Fire year (2000-2001)			***Stage at time t***		
(B_1)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0	0.460	0.856
Medium ramet (10-30cm)	0	0	0	0.570	1.457
Large ramet (>30cm)	0	0	0	0.015	0.143
1 yr. post-fire (2001-2002)					
(B_2)					
Stage at time t+1					
Seedling	0	0	0	0	0.164
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.180	0.007	0.404
Medium ramet (10-30cm)	0	0	0.360	0.481	0
Large ramet (>30cm)	0	0	0	0.351	1
2 yrs. post-fire (2002-2003)					
(B_3)					
Stage at time t+1					
Seedling	0	0	0	0	0.164
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0.646	0	0.385	0.140	0.343
Medium ramet (10-30cm)	0.085	0	0.154	0.562	0.275
Large ramet (>30cm)	0	0	0	0.2	0.788

Table A.2 continued

Wood Addition Population

Fire year (2000-2001)			***Stage at time t***		
(B_1)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+1		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0	0
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0	0.317	0.718
Medium ramet (10-30cm)	0	0	0.200	0.721	2.026
Large ramet (>30cm)	0	0	0	0.012	0.100
1 yr. post-fire (2001-2002)					
(B_2)					
Stage at time t+1					
Seedling	0	0	0	0	0.166
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.111	0.004	0.404
Medium ramet (10-30cm)	0	0	0.278	0.551	0
Large ramet (>30cm)	0	0	0	0.245	1
2 yrs. post-fire (2002-2003)					
(B_3)					
Stage at time t+1					
Seedling	0	0	0	0	0.166
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0.548	0	0	0.111	0.462
Medium ramet (10-30cm)	0.129	0	0	0.430	0.374
Large ramet (>30cm)	0	0	0	0.063	0.643

Table A.3 All 3-year periodic matrices ($\mathbf{A}_1=\mathbf{B}_3*\mathbf{B}_2*\mathbf{B}_1$) used in the *Rhus copallina* demography study in Chapter 4. Each matrix projects a treatment subpopulation over 3 years from fire in year one through two subsequent post-fire years.

Control Population

(A_1)			***Stage at time t***		
(2000-2003)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+3		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0.002	0.084	0.165
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.008	0.112	0.223
Medium ramet (10-30cm)	0	0	0.032	0.311	0.467
Large ramet (>30cm)	0	0	0.016	0.433	0.812

Fine Fuel Removal Population

(A_1)			***Stage at time t***		
(2000-2003)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+3		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0.0018	0.0714	0.1315
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.005	0.042	0.080
Medium ramet (10-30cm)	0	0	0.060	0.350	0.536
Large ramet (>30cm)	0	0	0.011	0.328	0.598

Pine Needle Addition Population

(A_1)			***Stage at time t***		
(2000-2003)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+3		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0	0.035	0.107
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0	0.173	0.466
Medium ramet (10-30cm)	0	0	0	0.321	0.783
Large ramet (>30cm)	0	0	0	0.257	0.717

Wood Addition Population

(A_1)			***Stage at time t***		
(2000-2003)	Seedling	Clonal ramet	Small ramet	Medium ramet	Large ramet
Stage at time t+3		(new)	(<10 cm)	(10-30 cm)	(>30 cm)
Seedling	0	0	0.008	0.031	0.099
Clonal ramet (new)	0	0	0	0	0
Small ramet (<10cm)	0	0	0.035	0.142	0.430
Medium ramet (10-30cm)	0	0	0.066	0.279	0.791
Large ramet (>30cm)	0	0	0.038	0.151	0.466

VITA

Jarrod Matthew Thaxton was born December 15, 1972, in Baton Rouge, Louisiana, to Sandra Martin and Ronnie Thaxton. He grew up near East Fork, Mississippi, and attended Liberty Elementary School until he was 11 years old. Jarrod's desire to be an ecologist dates to these early years and was sparked by long walks through the pine woods of Amite County with his grandfather, Victor J. Martin. His family then moved to Oxford, Mississippi, where he graduated from Oxford High School in 1991. In 1995, Jarrod graduated from Princeton University with a degree in ecology and evolutionary biology. While at Princeton, he completed a senior thesis on tropical forest understory light environments under the direction of Dr. Stephen P. Hubbell. After graduation, he spent a year as a research assistant at the Smithsonian Tropical Research Institute field station on Barro Colorado Island, Panama. While there he worked under the supervision of Drs. Allen Herre and Jenny Davidson on the effects of fungal pathogens on the population genetics of tree seedlings. In 1996, he entered the Department of Plant Biology at Louisiana State University and began a doctoral program under the supervision of Dr. William J. Platt.